Potential evolutionary responses to landscape heterogeneity and systematic environmental trends

Mögliche evolutionäre Reaktionen auf Landschaftsheterogenität und systemische Umwelttrends

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Nothing in biology makes sense
except in the light of evolution
—Theodosius Dobzhansky

Summary

Over the course of the last century, humans have witnessed drastic levels of global environmental change that endangered both, the survival of single species as well as biodiversity itself. This includes climate change, in both environmental means and in variance and subsequently frequent extreme weather events, as well as land use change that species have to cope with. With increasing urbanization, increasing agricultural area and increasing intensification, natural habitat is not only lost, but also changes its shape and distribution in the landscape. Both aspects can heavily influence an individual's fitness and therefore act as a selective force promoting evolutionary change. This way climate change influences individuals' niches and dispersal. Local adaptation and dispersal are not independent of each other. Dispersal can have two opposite effects on local adaptation. It can oppose local adaptation, by promoting the immigration of maladapted individuals or favor local adaptation by introducing better adapted genotypes. Which of those effects of dispersal on local adaptation emerges in a population depends on the dispersal strategies and the spatial structure of the landscape. In principle an adaptive response can include adjustment of the niche optimum as well as habitat tolerance (niche width) or (instead) ecological tracking of adequate conditions by dispersal and range shifting. So far, there has been no extensive modeling study of the evolution of the environmental niche optimum and tolerance along with dispersal probability in complex landscapes. Either only dispersal or (part of) the environmental niche can evolve or the landscapes used are not realistic but rather a very abstract representation of spatial structures.

I want to try and disentangle those different effects of both local adaptation and dispersal during global change, as well as their interaction, especially considering the separation between the effects of increasing mean and increasing variance. For this, I implemented an individual based model (IBM), with escalating complexity. I showed that both on a temporal as well as on a spatial scale, variation can be more influential then mean conditions. Indeed, the actual spatial configuration of this heterogeneity and the relationship between spatial and temporal heterogeneity affect the evolution of the niche and of dispersal probability more than temporal or spatial mean conditions.

I could show that in isolated populations, an increase of an environmental attribute's mean or variance can lead to extinction, under certain conditions. In particular, increasing variance cannot be tracked forever, since

increasing tolerance has distinct limits of feasibility. Increasing mean conditions can also occur too fast to be tracked, especially from generalist individuals. When expanding the model to the metapopulation level without a temporal environmental trend, the degree of spatial vs. temporal heterogeneity influenced the evolution of random dispersal heavily. With increasing spatial heterogeneity, individuals from extreme and rare patches evolve from being philopatric to dispersive, while individuals from average patches switch in the opposite direction. With the last expansion to a different set of landscapes with varying degrees of edge density, I could show that edge effects are strong in pseudo-agricultural landscapes, while in pseudo-natural habitats they were hardly found, regardless of emigration strategy. Sharp edges select against dispersal in the edge patches and could potentially further isolate populations in agricultural landscapes.

The work I present here can also be expanded further and I present several suggestions on what to do next. These expansions could help the realism of the model and eventually shed light on its bearing on ecological global change predictions. For example species distribution models or extinction risk models would be more precise, if they included both spatial and temporal variation. The current modeling practices might not be sufficient to describe the possible outcomes of global change, because spatio-temporal heterogeneity and its influence on species' niches is too important to be ignored for longer.

Zusammenfassung

Im Laufe des letzten Jahrhunderts wurde die Menschheit Zeuge von globaler Veränderungen in ungeahntem Ausmaß, die sowohl das Überleben einzelner Spezies als auch die Biodiversität an sich gefährden. Diese Veränderungen beinhalten Klimawandel, un zwar im Mittel als auch in der Varianz von Umweltparametern wie Temperatur od Niederschlag. Damit einher kommen auch immer häufigere Wetterextreme. Außerdem gehen natürliche Habitate durch Landnutzungsänderungen, durch zunehmende Urbanisierung, Agrarisierung und Intensivierung der Landwirtschaft verloren und ihre Form und Verteilung ändern sich. Mit beidem Aspekten der Umweltänderung müssen Spezies zurecht kommen um zu überleben, da beide die individuelle Fitness beeinflussen und daher als selektive Kraft bei der Anpassung an die Umwelt wirken können. Dadurch beeinflusst globale Veränderung die ökologische Nische und Ausbreitungsfähigkeit von Arten. Lokale Anpassung und Ausbreitungsfähigkeit sind voneinander abhängig, da die Ausbreitung zwei gegensätzliche Effekte auf die Anpassung von Individuen haben kann. Entweder wirkt sie lokaler Anpassung entgegen, da schlecht angepasste Individuen in Populationen einwandern, oder fördert lokale Anpassung durch selektive Einwanderung von gut angepassten Individuen. Welcher dieser Effekte auftritt, hängt sowohl von der Ausbreitungsstrategie als auch von der Struktur der Landschaft ab. Bisher hat es noch keine ausführlichen Modellierstudien über die parallele Evolution von lokaler Anpassung im Nischenoptimum und der Umwelttoleranz als auch von Ausbreitungsfähigkeit in komplexen Landschaften gegeben. Entweder kann nur die Ausbreitungsfähigkeit oder nur die Nische (in Teilen) evolvieren oder die Landschaften sind nicht realistisch sondern stark abstrahierte Representationen der räumlichen Strukturen.

In meiner Doktorarbeit versuche ich, die verschiedenen Effekte von lokaler Anpassung und Ausbreitungsfähigkeit unter globaler Veränderung, und ihre möglichen Interaktionen zu entwirren. Besonderes Augenmerk lege ich auf die Trennung von Anstieg im Mittelwert und Anstieg in der Varianz. Dafür implementierte ich ein Individuen-basiertes Modell (IBM) mit ansteigender Komplexität. Ich konnte zeigen, dass sowohl räumlich als auch zeitlich gesehen, ein Anstieg der Varianz mehr Einfluss haben kann, als die mittleren Konditionen. Tatsächlich beinflussen die räumliche Konfiguration dieser Heterogenität und das Verhältnis von räumlicher zu zeitlicher Varianz die Evolution der ökologischen Nische und der Ausbreitungsfähigkeit mehr, als räumliche oder zeitliche Mittelwerte.

Ein Anstieg des Mittelwertes und der Varianz von Umweltattributen kann zum Austerben von isolierten Populationen führen, zumindest unter bestimmten Voraussetzungen. Ansteigende Varianz kann nicht unbegrenzt evolutionär ausgeglichen werden, da eine Steigerung der Habitattoleranz mit Kosten verbunden ist, die ultimativ eine unbegrenzte Ausweitung der Nische verhindern. Ein ansteigender Mittelwert kann ebenfalls zu schnell erfolgen, als dass er verfolgt werden könnte, vor allem von Generalisten.

Nach der Erweiterung des Modells zu einer Metapopulation ohne zeitliche Trends konnte ich zeigen, dass das Verhältnis von räumlicher zu zeitlicher Varianz ausschlaggebend ist für die Evolution von zufälliger Ausbreitung. Mit ansteigender räumlicher Heterogenität, wechseln Individuen in extremen und seltenen Habitaten von Philopatrie zu häufigen Auswanderungen, während Individuen aus durchschnittlichen Habitaten sich genau andersherum verhielten.

Die letzte Erweiterung des Modells war Landschaften mit unterschiedlicher Kantendichte zu verwenden. Hier konnte ich zeigen, dass die Randeffekte in pseudo-landwirtschaftlichen Landschaften sehr stark waren, während keine in pseudo-natürlichen Landschaften auftraten, unabhängig von der Emigrationsstrategie. Scharfe Kanten selektieren für geringe Ausbreitung und könnten für Populationen in landwirtschaftlichen Gegenden eine noch stärkere Isolation bedeuten.

Meine Untersuchungen können noch ausgeweitet werden und ich präsentiere einige Vorschläge, was als nächstes angegangen werden könnte. Diese Erweiterungen könnten den Realismus des Modells weiter voran treiben und schlussendlich helfen, Vorhersagen zur globalen Veränderung zu verbessern. Beispielweise könnten Artverteilungsmodelle oder Austerberisikomodelle präziser werden, wenn sie räumliche und zeitliche Varianz einschließen würden. Die aktuellen Modelle könnten nicht ausreichend sein, die möglichen Konsequenzen der globalen Veränderungen zu beschreiben, da räumliche und zeitliche Heterogenität und ihr Einfluss auf die Evolution der ökologischen Nische und Ausbreitungsfähigkeit zu wichtig ist, um weiter ignoriert zu werden.

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I | Introduction

1 | Global environmental change

Over the course of the last century, humans have witnessed drastic levels of global environmental change that endangered both, the survival of single species as well as biodiversity itself (IPCC 2014; Potts et al. 2016). This environmental change includes, among others, climate change as well as land use change that species have to cope with.

Climate change includes change in both environmental means and in variance. Prominently and exemplarily, an increase in environmental mean can be found in the global increase in mean temperature (IPCC 2014). Climate change not only leads to an increase in mean temperature, but also to a rising temperature variance (Alexeeff et al. 2018; Crhová et al. 2018; Fischer and Schär 2008; IPCC 2014; Lenton et al. 2017; Scherrer et al. 2005; Wang and Dillon 2014) and subsequently to more frequent extreme weather events (Easterling et al. 2000; Kingsolver and Buckley 2017; Rummukainen 2012; Ummenhofer and Meehl 2017). Changes in precipitation frequency and patterns are also predicted (Bergholz et al. 2017; IPCC 2014). Most research on how species may adapt to or cope with such changes has focused on the effects of changing mean temperature (Bailey and Pol 2016; Bozinovic et al. 2011; Clusella-Trullas et al. 2011; David et al. 2017; Dillon and Woods 2016; Paaijmans et al. 2013). In the last years however, the number of empirical studies investigating also the effects of temperature variance is increasing. An increase in variance in the environmental parameter can lead to a higher occurrence probability of adverse conditions and extreme climatic events (but see Bailey & van de Pol (2016)).

In addition to the climatic component of global environmental change, it also includes the change of landscape structures via land use change. With increasing urbanization, increasing amount of land area used for agriculture and increasing intensification, natural habitat is not only lost , but also changes its shape and distribution in the landscape (Crooks et al. 2017; Crowley et al. 2019; Homola et al. 2019; Liira et al. 2008; Mapelli et al. 2020; Ribeiro et al. 2019). Since there is almost no way to survive complete habitat loss, the interesting question remains how species might adapt to habitat fragmentation and change of transition zones (ecotones). Habitat fragmentation disconnects metapopulations (Homola et al. 2019; Matter et al. 2020) and hinders the functional connectivity of different types of habitats necessary for a species' survival (e.g. that between breeding and feeding sites) (Ribeiro et al. 2019). With increasing fragmentation the amount of edges between habitats also rises, leading to more edge effects (Crooks et al. 2017). Higher edge density was shown to correlate with agricultural landscapes with low species richness (Liira et al. 2008). Even when natural habitat is protected or retained, the ecotone between habitats is often less gradual in agricultural landscapes, which can have a detrimental effect on species (Vespa et al. 2018).

2 | Climate change influences niche

Both aspects of climate change mentioned in the previous chapter can heavily influence a species' or individual's fitness and therefore act as a selective force during adaptation to the environment. This can be considered an eco-evolutionary feedback, by which climate change also influence individual's niches. (Bartheld et al. 2017; Briga and Verhulst 2015; David et al. 2017; Folguera et al. 2009; Paaijmans et al. 2013; Shama 2015). The environmental niche is described by the multidimensional environmental parameter space that can be occupied by a species. The environmental parameters can be abiotic and biotic, but here I focus on abiotic factors, such as temperature, pH-level or other continuous variables. The niche of a species for a single environmental parameter (as I consider it here), is determined by the location of the niche center, i.e. where the species' (viz. individual's) fitness is highest and the deviation around this optimum, where the species can still strive, but with lower fitness. The magnitude of this deviation is considered the niche width or tolerance of a species. In general, the environmental niche of a species is assumed to be fixed but intraspecific variation allows individuals from a species to have slightly varying niche optima and widths, and therefore have a higher fitness (number of offspring) under different environmental conditions (across the parameter space) (Pocheville 2015). This enables selection of different phenotypes . By this mechanism, evolution of a species' niche is possible: If individuals with a niche that deviates from the species' average niche have a (systematically) higher number of offspring under changing conditions, the proportion of this phenotype in the population becomes higher. Individuals (viz. species) with

a low tolerance are usually considered specialists and are expected to have a high fitness (high maximum number of offspring) in optimal conditions, but are more susceptible to conditions that deviate from the optimum. In contrast, generalists have a high environmental tolerance but lower fitness in optimal conditions. Even though these properties are usually determined at the species level, intraspecific variation in environmental tolerance exists as well. This was recently shown for different genotypes of the plant *Ara-*

bidopsis thaliana (J F Scheepens et al. 2018a). More so, population level plasticity can also emerge through variability between individuals, with different genotypes in different places in the species' spatial and temporal range (Cobben, Verboom, et al. 2012).

To survive an changing mean in environmental conditions, individuals (viz. species) have several potential ways of responding: If the increase in mean is not too pronounced, it might still fall inside the indiviudals' niche width. This way, they can endure such change. Nevertheless, if the increase in mean becomes persistent or even continues , it is most likely, that the individuals' tolerance cannot cover it anymore, or the decrease in fitness is too pronounced to be sustainable for longer periods of time. Then individuals can either leave their habitat to hopefully find a more suitable one, or selection might work in the populations' favor and select the individuals with a better fitting niche optimum. This would then enable the populations to evolutionarily track the environmental change. In the latter case of local adaptation, the whole niche is shifted in it's position in the environmental spectrum. Local adaptation also emerges without climate change, when populations of the same species differ in their phenotypes between locations. The differing environmental conditions between sites were shown to influence trait plasiticity in phenology, growth, reproduction and allocation strategy. Plasticity in those traits increased with increasing precipitation variability (Fournier-Level et al. 2011; J F Scheepens et al. 2018a).

Some experiments show that increasing environmental variance can in fact be more detrimental than just an increasing mean or even change the effects of an increasing mean. For several taxa, the detrimental effect of rising environmental variability on fitness have been observed, e.g. arthropods (David et al. 2017; Folguera et al. 2009; Paaijmans et al. 2013), birds (Briga and Verhulst 2015) and amphibians (Bartheld et al. 2017). A few studies also show that species are able to acclimate to temperature variability and actually gain fitness from exposure to variable conditions (Bozinovic et al. 2011). In an experiment on the invasibility of t*Arabidopsis thaliana* genotypes under thermal variability a positive effect on the resistance against a competing species was found (J. F. Scheepens et al. 2018b). In some cases, as described by Benedette-Cecchi et al. (2006), the effects of increasing temperature variability can interact with those of increasing mean and lead to diverging results, depending e.g. on species and ecological niche. Overall, there‘s no denying of the influence of increasing thermal variability on species‘ fitness (Vázquez et al. 2017). Similar arguments can also be applied when considering changes other than climatic ones, e.g. precipitation, soil nutrient value or pH, that can influence the fitness of species. For example, Wahl at al. (2016), show that in ocean acidification, caused by climate change, the variance in pH of the system influences the biome strongly. To adapt to increasing environmental variability, species might have no choice but to increase their niche width, which can have huge effects on their fitness, given a specialist-generalist trade-off exists. It is often assumed that such a trade-off has to exist, since without it, there would not be any biodiversity on earth. If it were possible for a species to become the perfect generalist, tolerating all environmental conditions that might exist on earth, without loosing fitness, this species would have taken over all biomes by now and we would not find other species. Additionally from a physiological point of view, development of tolerance is associated with costs. If a species (or individual) were to be tolerant to a wider range of e.g. temperatures, it needs some kind of either heat stress resistance or cold resistance. This is usually linked to certain protective proteins and linked to physiological costs (Huey and Hertz 1984; Luhring and DeLong 2017; Ørsted et al. 2018). Other similar cases can probably be found for most environmental attributes. The existence of a specialist-generalist trade-off was also confirmed empirically, e.g. in Jurriaans S. and Hoogenboom M. O. 2019; Nguyen et al. 2019.

Overall, the increase in environmental variability can have a bigger and more complex influence on the fitness of individuals and therefore evolution of species than just a change in mean conditions.

3 | Landscape structure influences niche and dispersal

Local adaptation and dispersal obviously are not independent of each other but interact and shape each other. Dispersal can have two opposite effects on local adaptation. It can oppose local adaptation, by promoting the immigration of maladapted individuals especially when dispersal is random. Random dispersal can therefore promote the evolution of generalists and hinder the emergence of habitat specialists (Kisdi 2002; Mortier et al. 2018; Stevens et al. 2014). In particular during range shift, dispersal may lead to colonization by maladapted individuals at the range front (Cobben, Verboom, et al. 2012). The same can be said for patches which are spatially disconnected from the core habitat and that depend on immigration for continuous occupation (sink patches). Here the asymmetric gene flow from source patches (core habitat) can lead to local maladaptation (Kawecki 2008; Sinai et al. 2019). Weiss-Lehmann and Shaw (2020) could show that in sexually reproducing species, increased dispersal can lead to gene swamping via increased gene flow and therefore reduce local adaptation. Apart from the fitness reduction caused by the immigration of maladapted individuals, dispersal also influences the trait distribution of populations. It can change both the mean trait values, but also influence the trait variability, by changing the frequency of certain traits (Bridle et al. 2019). This again can hinder local adaptation.

On the other hand, dispersal can also favor local adaptation. If a dispersing individual can choose its new habitat, this can lead to a better match between phenotype and habitat properties. This can then promote local adaptation of a population, because it increases the proportion of individuals with a habitat matching phenotype(Camacho et al. 2020; Jacob, Laurent, Haegeman, et al. 2018; Kisdi et al. 2020). In turn, this can then further promote dispersal, since the advantages (e.g.avoidance of kin-competition and inbreeding depression) outweigh the disadvantages because the risk of being maladaptated in the target habitat becomes marginal. This can then select for highly dispersive specialists (Jacob, Laurent, Haegeman, et al. 2018). Habitat choice was also shown to evolve faster than local adaptation (Kisdi et al. 2020), which, in combination with the before mentioned feedback loop, speed up local adaptation. Further, dispersal can also increase the genetic variation, which increases evolutionary potential (Bridle et al. 2019).

Which of those effects of dispersal on local adaptation emerges in a population consequently depends on the dispersal strategies. Additionally, it also depends on the spatial structure of the landscape the metapopulation inhabits. Linear environmental gradients, as well as sharp edges between habitats (transition zones between neighboring habitats) can hinder or select against dispersal, while nonlinear gradients and soft edges promote dispersal (Bridle et al. 2019; Vespa et al. 2018).

4 | Research goals

So far, there has been no extensive study of the evolution of the environmental niche optimum and tolerance along with dispersal probability in complex landscapes. Either only dispersal or (part of) the environmental niche can evolve or the landscapes used are not realistic but rather a very abstract representation of spatial structures. Evolution in both niche optimum and niche width has not been sufficiently studied in general and the possible interactions with dispersal even less. "Landscapes" often only change in one dimension (gradient landscapes), exhibit highly simplified patterns (checkerboard landscapes) or consist of a dual combination of matrix and inhabitable patches. Therefore, local adaptation as found in natural populations was not possible to explore in these landscapes. Considering all of the above mentioned patterns, it seemed interesting to try and disentangle the different effects of both local adaptation and dispersal during global change, as well as their interaction with each other. I wanted to use this doctoral thesis to try and disentangle the separate effects of climate change and of landscape structure on the evolution of both the environmental niche and dispersal of organisms. Especially the separation between increasing mean and increasing variance were of interest.

I wanted to examine the effects of

1) temporal heterogeneity and its systematic temporal trends in both variance and mean on the environmental niche
2) spatial heterogeneity and the distribution of environmental conditions on the environmental niche and emigration probability
3) spatial heterogeneity and the spatial structure of landscapes on the environmental niche and emigration probability
4) emigration strategy on the environmental niche and emigration rate.

II | Main

5 | Environmental change and variability influence niche evolution of isolated natural populations

We first focused on the influence of temporal variability on the environmental niche. In the following manuscript, we tried to disentangle the effect of an increasing environmental mean and an increasing environmental variation on the evolution of the evironmental niche. To exclude possible confounding effects of dispersal, we first considered an isolated population without emigration or immigration.
The manuscript was pusblished in *Regional Environmental Change* (Sieger et al. 2019). I implemented the simulation model, performed all analysis and, drafted and wrote the manuscript. Thomas Hovestadt conceptualized the research and contributed to the manuscript. Marleen Cobben also contributed to the manuscript. My overall contribution amounted to ca. 90%.

5.1 Abstract

Most organisms face variable environmental conditions. Strategies to cope with such variation are e.g. bet-hedging, dispersal, or tolerance. With a systematic trend in temperature or other environmental characteristics, e.g. under climate change, species also experience selection pressure towards a changing environmental optimum. Here we simulate the evolution of niche optimum and width (tolerance) in isolated populations, under different scenarios: 1. environmental conditions are static (constant mean and standard deviation; control) or follow a trend in 2. the mean, 3. the variance, or 4. in both, simulating the predicted effects of climate change. Tolerance trades off against maximum fertility (fitness). Results show that populations can evolutionarily track a trend in mean conditions as long as change does not proceed too fast. An increase in variance, however, can be more detrimental, due to the inherent trade-offs associated with enlarging tolerance. Indeed, for any given trade-off a theoretical upper boundary exists for the evolution of tolerance: if environmental variance becomes too large, populations cannot evolve sufficient tolerance and go extinct. An increasing variance can never be tracked indefinitely if a trade-off as assumed here exists. Importantly, climate change models often focus on the impact of increasing mean temperatures only. Here we show that including the projected increase in environmental variance may change results considerably.

5.2 Introduction

Climate research shows that climate change not only leads to an increase in mean temperature, but also to an increase in its variance (Alexeeff et al. 2018; Crhová et al. 2018; Fischer and Schär 2008; IPCC 2014; Lenton et al. 2017; Scherrer et al. 2005; Wang and Dillon 2014) and subsequently to more frequent extreme weather events (Easterling et al. 2000; Kingsolver and Buckley 2017; Rummukainen 2012; Ummenhofer and Meehl 2017). Changes in precipitation frequency and patterns are also predicted (Bergholz et al. 2017; IPCC 2014). Most research on how species may adapt to or cope with those changes has focused on the effects of mean temperature (Bailey and Pol 2016; Bozinovic et al. 2011; Clusella-Trullas et al. 2011; David et al. 2017; Dillon and Woods 2016; Paaijmans et al. 2013). In the last years however, the number of empirical studies investigating also the effects of temperature variance is increasing. An increase in variance in the environmental parameter can lead to a higher occurrence probability of adverse conditions and extreme climatic events (but see Bailey & van de Pol (2016)). Experiments show that increasing environmental variance can in fact be more detrimental than just an increasing mean or even change the effects of an increasing mean. Folguera et al. (2009) showed that in woodlice, increasing temperature variability affected performance traits differently than an increase in mean temperature; most importantly, survival declined more rapidly with increasing temperature variance. David et al. (2017) came to similar conclusions while studying the influence of increasing temperature variance on the longevity of black pine sawyer beetles (textitMonochamus galloprovincialis). Under temperatures with identical means but different variances, the beetles exposed to higher between-day variances survived shorter. A similar negative fitness effect was found in tadpoles: exposed to daily temperature fluctuations, their maximum swimming speed, used as a proxy for fitness, was lower than if kept under constant water temperatures (Bartheld et al. 2017). It was further shown, that ectotherms‘ reproductive strategies (Shama 2017) as well as their susceptibility to thermal variance (Paaijmans et al. 2013) are highly influenced by temperature variability. A similar pattern can also be found in birds, where the thermal tolerance is influenced by the thermal variability (Briga and Verhulst 2015). However, some studies also show that species are able to acclimate to temperature variability and actually gain fitness from exposure to variable conditions. For example, *Drosophila melanogaster* recover faster from heat coma and survive heat exposure better when reared under fluctuating, warm temperatures than when reared under constant warm temperatures (Bozinovic et al. 2011). In an experiment on the invasibility of t*Arabidopsis thaliana* genotypes under thermal variability a positive effect on the resistance against a competing species was found (J F Scheepens et al. 2018a). In some cases, as described by Benedette-Cecchi et al. (2006), the effects of increasing temperature variability can interact with those of increasing mean and lead to diverging results, depending e.g. on species and ecological niche. Overall, there‘s no denying of the influence of increasing thermal variability on species‘ fitness (Vázquez et al. 2017). However, empirical data is only available over (evolutionarily) short time spans and the thermal variance investigated also differs in its thermal and temporal scope. Some studies include daily fluctuations during a year, some focus more on seasonal variation across several years but none show the influence of inter-annual variation over many generations.

It is not only the variation in temperature but also in other environmental parameters, such as precipitation, soil nutrient value or pH, that can influence the fitness of species. For example, Wahl at al. (2016), show that in ocean acidification, caused by climate change, the variance of the system influences the biome strongly and needs to be included in future research of species' adaptation to this acidification. To deal with the unavoidable variance of any environmental factor, single organisms (but also populations) can (and must) express a certain tolerance against such variance around their environmental (niche) optimum. Generally, the ecological niche is described by the multidimensional environmental parameter space that can be occupied by a species. These environmental parameters can be abiotic and biotic, but here we focus on abiotic factors, such as temperature, pH-level or other continuous variables. The niche of a species for a single environmental parameter (as we consider it here), is determined by the location of the niche center, i.e. where the species' fitness is highest and the deviation around this center, where the species can still survive, but with lower fitness. This deviation is considered the niche width or tolerance of a species. In general, the ecological niche of a species is assumed to be fixed, however intraspecific variation allows individuals from a species to have slightly different niche optima and widths, and therefore have a higher fitness (number of offspring) under different environmental conditions (across the parameter space) (Pocheville 2015). This enables selection of different phenotypes in this species. By this mechanism, evolution of a species' niche is possible: If individuals with a niche that deviates from the species' aver-

age niche have a higher number of offspring under changing conditions, the proportion of this phenotype in the population becomes higher. Individuals (viz. species) with a low tolerance are usually considered specialists and are expected to have a high fitness (high maximum number of offspring) in optimal conditions, but are more susceptible to conditions that deviate from the optimum. In contrast, generalists have a high environmental tolerance but lower fitness in optimal conditions. Even though these properties are usually determined at the species level, intraspecific variation in environmental tolerance exists as well. This was recently shown e.g. for different genotypes of the plant *Arabidopsis thaliana*, where Scheepens et al. (2018) found genotypes with a higher heat stress tolerance to have lower fitness at optimum conditions compared to less tolerant genotypes. More so, population level plasticity can also emerge through variability between individuals, with different genotypes occupying different places in the species' spatial and temporal range (Cobben, Verboom, et al. 2012).
A fundamental assumption of life-history theory is the existence of inherent trade-offs between resource-based life-history traits (King, Daphne J. Fairbairn, et al. 2012; D. A. Roff and D. J. Fairbairn 2007). It can thus be assumed that in the specialist-generalist systems described above, a trade-off exists as well, because adults only have a finite amount of resources to allocate to offspring or into higher stress-resistance against non-optimal conditions (tolerance) in a given environment (e.g. Rutschmann et al. 2016). With increasing tolerance the number of offspring in adverse conditions increases, whereas the maximum number of offspring at optimal conditions declines (e.g. J F Scheepens et al. 2018a). Under which climatic conditions, including increasing variability, which strategy (tolerance) is favored to maximize number of offspring is not established yet. Widening the niche and thus becoming more tolerant (becoming a generalist) is one strategic response to overcome an increase in environmental variance. Cobben et al. (2012) already showed that in environments with a higher variability populations have a higher proportion of generalists. Yet it would also be possible to spread the risk of encountering adverse conditions by dispersing to more suitable habitats, developing dormancy to avoid environmental extremes (Ellner and Shmida 1981), or distribute risks by creating offspring with different phenotypes (Bergholz et al. 2017). As Vasseur et al. (2014) stated, it is difficult to trace the full extent of the influence of thermal variability, since individuals and species experience it on so many scales, ranging from diurnal to seasonal to inter-annual thermal variation (Crhová et al. 2018). To explore the effects of long-term changes

in temperature and other abiotic environmental parameters we often rely on analytical or simulation models, e.g. in population dynamics models. These models typically focus, however, on the increasing mean and seldom incorporate or consider the increase in variance also predicted (Bailey and Pol 2016; Lawson et al. 2015). Consequently, several reviews have called to pay more attention to the effect of an increase in temperature variability in both theoretical and empirical studies (Lawson et al. 2015; Sofaer et al. 2017; Vasseur et al. 2014; Vázquez et al. 2017).

One examples of a model indeed incorporating the influence of both, an increase in mean and variance is Vincenzi (2014), who could show, that an increase in climate variability and climate mean increased the risk of extinction and decreased the time to extinction. Vincenzi showed that populations could adapt to a trend in the environmental mean (with a given selection strength), but not to an increase in climate variability. However, Vincenzi's model did not allow adaptation of the niche width - niche width (tolerance) was set to a pre-defined value thus representing the strength of selection in an variable environment. For an increase in environmental variance however, a certain tolerance is crucial, since it enables individuals to endure environmental extremes. Tolerance may thus itself be a trait under selection.

To fill this knowledge gap, we aim to investigate the influence of a long-term trend of increasing mean and/or variance of an environmental parameter on the evolution of the ecological niche and the longevity of populations. To explore the evolution of niches, accounting for intraspecific variation of traits is paramount. In other words, we need to present a population of individuals that differ in their attributes. This can readily be done in so called "individual based models", where the core unit of simulation are individuals. Such models usually simulate individual attributes, such as reproduction, survival, movement, or other behaviors, to understand population level phenomena.

Here we simulated the eco-evolutionary dynamics of a single population with individuals' niches requirements varying in both their optimum and environmental tolerance, in a habitat with an inter-annual increase in the mean, variance or both of an environmental parameter. This approach also follows the call for more models including evolving plasticity (here included as evolving habitat tolerance) in assessments of population dynamics under climate change (Romero-Mujalli et al. 2018). We hypothesize, that (1) an increasing mean of an environmental parameter can – provided the change does not occur too fast – 'eternally' be tracked by adapting the niche optimum, (2) that increasing variance will lead to evolution of increasing environmental tolerance, but (3) that, because of inherent trade-offs increasing tolerance comes at the cost of a decreasing number of offspring at optimal conditions.

5.3 Material and Methods

5.3.1 General model structure

Population dynamics. We simulate an isolated population of N_t annual, haploid individuals in a habitat with a temporally variable environmental attribute H_t. This attribute can most easily be interpreted as temperature, but could also represent other fitness-relevant, continuous abiotic factors, such as salinity, soil nitrogen level, or pH-level. In all simulations the attribute underlies uncorrelated inter-annual variability by drawing for each time step (year) values from a normal distribution with specified and – depending on scenarios (see below) – time dependent values for the mean and standard deviation (sd) of temperature. H_t influences any individual's fertility, depending on the individual's attributes: individuals carry two heritable traits, coding for the individual's habitat optimum h_i and its tolerance, g_i. Note that, even though the tolerance trait is here described as niche width, it can also be interpreted as phenotypic adaptation or plasticity as the environmental variation considered is inter-generational. Habitat optimum and environmental tolerance can evolve by selection and adaptation (see below). Simulation scenarios are further characterized by a trade-off parameter α that defines the fitness cost (penalty) T_h associated with increasing tolerance by damping maximum fitness under optimal conditions (following Chaianunporn and Hovestadt 2015), which can again also be interpreted as the fitness cost associated with phenotypic plasticity. There is little empirical support on how large α could be. The chosen values here cover the range from values that lead to populations just being able to survive the control scenario up to values that stabilize niche evolution (no further significant change in trait values, even with bigger values of α):

$$T_h = e^{\frac{-g_i^2}{2\alpha^2}} \tag{5.1}$$

Note that larger values of α imply lower trade-off costs. The resulting environment dependent expected number of offspring $L(H_t, g_i)$ for each adult i is calculated as:

$$L(H_t, g_i) = R_0 \cdot T_h \cdot e^{\frac{-(H_t-h_i)^2}{g_i^2}} \tag{5.2}$$

with R_0 the maximum possible offspring number (see supplementary information S2).

The actual number of offspring (larvae) for each adult i is generated by drawing from a Poisson-distribution with mean $L(H_t, g_i)$. The total larvae L_0 produced in the population then undergo density-dependent survival, with survival probability calculated according to the Beverton-Holt-model:

$$s_A = \frac{1}{1 + a \cdot L_0} \tag{5.3}$$

with $a = \frac{R_0-1}{K \cdot R_0}$ and K the carrying capacity. This survival probability is used to allocate a random binomial factor to each individual offspring indicating whether it survives or not; the surviving larvae constitute the adult population N_{t+1} of the next generation whereas all adults of the previous generation die. *Inheritance and mutation* Surviving offspring are either direct copies of their parent or can undergo, independently for either trait, mutation with probability 0.001. Both traits can mutate in the same time step. In case of mutation, the inherited value of the optimum h_i was modified by adding a random value drawn from a uniform distribution between -0.5 and 0.5. In case of mutating the tolerance trait the inherited value g_i was multiplied with a random value drawn from a uniform distribution between 0.5 and 1.5 to exclude the appearance of negative tolerance values. Additionally, we performed a sensitivity analysis to explore the simulation results of changing the parameters. Neither an increase or decrease in R_0, mutation probability, or mutation amplitude changed the qualitative outcome of the simulations. Similarly, Vincenzi (2014) reports no significant change in extinction risk or time to extinction with a change in mutation amplitude. (For the exact parameter combinations see supplementary information S3). It is therefore justified to assume the intermediate parameter values we chose here.

5.3.2 Initialization of simulations

To allow the populations to adapt traits h_i and g_i to prevailing non-changing habitat conditions, burn-in periods were run for five values of $\alpha \in 1, 1.5, 2, 3, 4$ over 1000 generations. These simulations were initialized with 10000 individuals, matching the carrying capacity K, and with values of H_0 drawn from a standard normal distribution. Individual traits were initialized with h_i drawn from a standard normal distribution and g_i drawn from a log-normal distribution with $\sigma_g = 1$ and $\bar{g} = 0$. Burn-ins for each value of α were replicated 100 times to gain sufficient data for initializing later simulation scenarios. Mean trait values, $\bar{h}$ and their standard deviation s_h as well as mean population size were recorded over the last 20 generations. To calculate parameters $\bar{g}$ and s_g of the log-normal distribution from the evolved trait values g_i, the means m and variance v of g_i were inserted into the calculation of the arithmetic moments of the log-normal distribution for mean (first moment, equation 5.4) and variance (second moment, equation 5.5):

$$\bar{g} = \ln\left(\frac{m}{\sqrt{1 + \frac{v}{m^2}}}\right) \tag{5.4}$$

and

$$\sigma_g^2 = \ln\left(1 + \frac{v}{m^2}\right) \tag{5.5}$$

In all following scenarios populations were initialized with an individual number similar to the mean number at the end of the corresponding burn-in simulations and with the individuals' trait values drawn from a Normal distribution for h_i and log-normal distribution for g_i with the corresponding parameters ($\bar{h}$ and s_h for trait h_i, and σ_g and $\bar{g}$ for trait g_i).

5.3.3 Scenarios

Four different environmental scenarios, all running over 300 generations were implemented. (i) A control scenario in which neither the mean nor the sd of temperature changed, but remained at the default values of $\bar{H}(t) = 0$ and $\sigma_H(t) = 1$ respectively. (ii) Mean trend scenarios, in which $\bar{H}(t)$ increased by a particular value $\delta(\bar{H})$ each generation (0.01, 0.02 or 0.03) whereas $\sigma_H(t)$ remained at its default value. (iii) Variance trend scenarios, with $\sigma_H(t)$ gradually increasing according to the same rules and with the same values $\delta(\sigma_H)$ as $\bar{H}(t)$ in scenario (ii) whereas $\bar{H}(t)$ remained at its default value of zero. And (iv) scenarios in which both $\bar{H}(t)$ and $\sigma_H(t)$ increased over time with the particular values ($\delta(\bar{H})$ and $\delta(\sigma_H)$) from the previous scenarios (0.01, 0.02 or 0.03). All possible combinations of annual increase were simulated. The values chosen for the scenarios are within e.g. predicted changes in mean temperature (scenario ii), precipitation (scenario iii) or variability of summer temperature (iv), but also see the discussion for further justification.

We ran each scenario for the five trade-off parameters of $\alpha \in 1, 1.5, 2, 3, 4$, leading to a total of 80 parameter combinations simulated (5*[1+3+3+9]) each replicated 100 times. Population dynamics did not change when increasing the trade-off parameter beyond $\alpha = 4$ (data not shown here) and consequently $\alpha = 4$ is the highest value necessary to explore our hypotheses.

5.3.4 Analysis

The influence of increasing mean and/or variance on survivorship of the populations was estimated by fitting a survival model to each scenario using statistical software R and the survreg() function from the "survival" R-package (Team 2018; Therneau 2015), 2015). For the mean plus variance trend scenario only the scenarios where the annual increase of $\bar{H}(t)$ and $\sigma_H(t)$ was the same were used for simplicity. For scenarios for which an estimation of mean survival time was not possible as no extinctions occurred in the simulation time of 300 years, we set values to the estimated survival time that would result if one population had gone extinct in year 300 (=30.000 years). Additionally, a survival model with the annual increase of $\bar{H}(t)$ and $\sigma_H(t)$ and the trade-off strength $\alpha \in 1, 1.5, 2, 3, 4$ as explanatory variables was fitted to all 80 scenarios, using again the survreg() function. The model output was then used to interpolate the mean survival time for all possible combinations of annual increases of $\bar{H}(t)$ and $\sigma_H(t)$ between 0 and 0.03 and for three values of $\alpha \in 1, 2, 4$ (Fig 2).
Assuming a temporally stable value of $\bar{H}(t)$ and $\sigma_H(t)$ the optimal tolerance $\hat{g}$ for any combination of $\sigma_H(t)$ and $\alpha \in 1, 1.5, 2, 3, 4$ can – for an infinite population size – be found numerically by estimating the long-term expected geometric mean fertility for any particular strategy g (see supplementary information S1). These numerical estimates serve as reference to compare with simulation results.

5.4 Results

The development of the population size over time in both the burn-in periods and the control scenarios showed that for all trade-off strengths a stable population could be established. In the control scenarios the population size stayed close to the carrying capacity for weak trade-off strengths , but settled at lower equilibrium sizes for more constraint populations . Overall, the estimated mean survival is much more sensitive to trends in the standard deviation $\delta(\bar{H})$ than in the environmental mean $\bar{H}$, as can

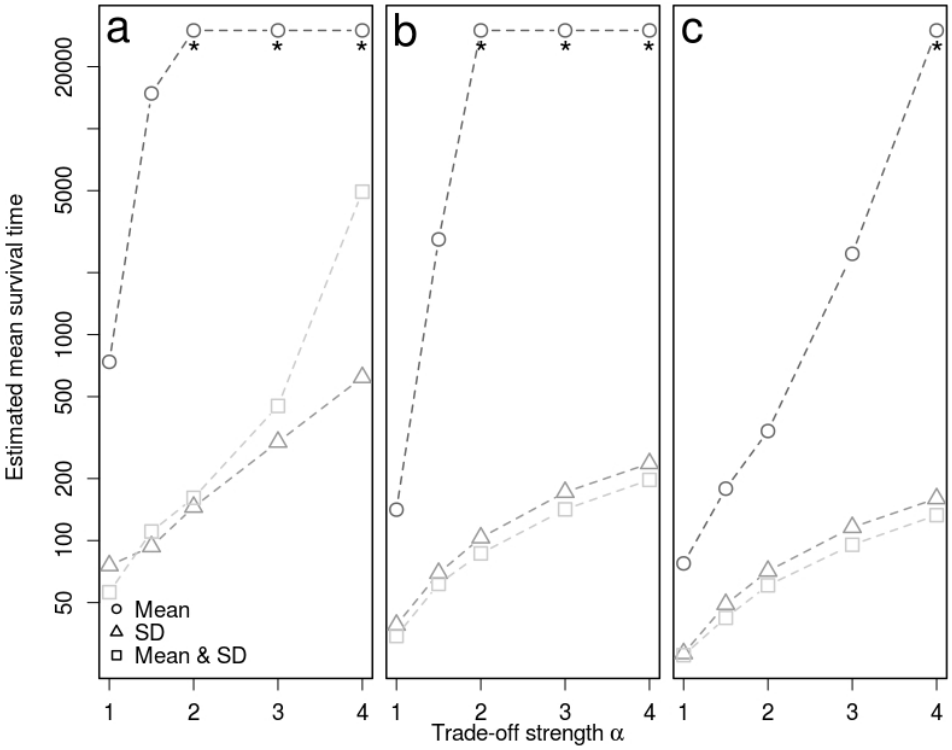

Figure 5.1: Estimated mean survival times in the three scenarios with an increase in mean $\bar{H}(t)$ (circles), standard deviation $\sigma_H(t)$ (triangles) and both (squares) for three different trend sizes $\delta(\bar{H}, \sigma_H) \in 0.01, 0.02, 0.03$ per generation in panel a), b) and c) respectively, over the five trade-off strengths of $\alpha \in 1, 1.5, 2, 3, 4$. In case of an increase in both $\bar{H}(t)$ and $\sigma_H(t)$, only scenarios with $\delta(\bar{H}(t)) = \delta(\sigma_H(t))$ were included. Low values of α indicate a stronger trade-off. Estimated mean survival time decreases with increasing $\delta(\bar{H}, \sigma_H)$ and increasing trade-off strength (decreasing α). Asterisks mark scenarios for which an estimation of mean survival time was not possible as no extinctions occurred in the simulation time of 300 years; we set values to the estimated survival time that would result if one population had gone extinct in year 300 (=30.000 years).

be seen in figure 1. In the scenarios with both an increase in mean and standard deviation, the latter has the dominating effect. Additionally, the trade-off strength is very critical: if the trade-off is strong (small values of α), populations survival is shorter (Fig. 5.1).

The results from the predicted mean survival times corroborate those findings. Median survival times for increases in only environmental mean are decidedly larger than for increases in environmental standard deviation or both. Again, the strength of the trade-off highly influences the outcome of the predictions: With increasing trade-off strength, populations survive shorter time spans (Fig 5.2).

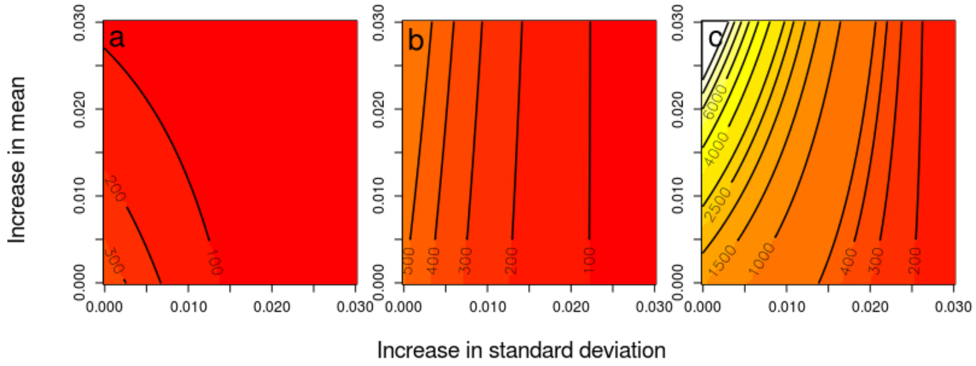

Figure 5.2: Predicted survival times interpolated for combinations of $\delta(\bar{H})$ and $\delta(\sigma_H)$ for three different values of the trade-off $\alpha \in 1, 2, 4$ (low values of α indicate strong trade-off) in panels a) b) and c) respectively. Contour lines show the predicted mean survival times.

In the control scenarios, for all trade-off strengths, an evolutionary equilibrium was reached, with the optimum trait h_i (obviously) approximating, with small deviations, the value of the environmental mean $\bar{H}(t) = 0$ and stable distributions of the tolerance trait g_i. Evolved tolerance was largest for a weak trade-off strength, and decreased with increasing trade-off strength. These values closely match the numerically calculated optimum values (supplementary information S1). A trend in the environmental mean (obviously) triggers an evolutionary response in the niche optimum with a characteristic adaptation gap forming as the trend set in. The magnitude of this gap depends on both, the speed of environmental change and the strength of the trade-off with larger gaps forming when the trade-off is weak (Fig. 5.3). Further, with slow trends and strong trade-offs the adaptation gap stabilizes at a characteristic size but with fast trends and particularly with weak trade-offs, the gap widens over the full simulation period.

Interestingly, the evolutionary response may not be in habitat optimum alone. In particular, when the trend is fast and the trade-off rather weak we also observe an (eventually massive) increase in habitat tolerance too (Fig. 5.4). However, neither evolutionary response can prevent population extinction when the trend in mean conditions is fast the trade-off is rather strong.

In the scenarios with only an increase in the standard deviation, optimum trait values did not change in comparison to the control scenarios and stayed close to the environmental mean. The tolerance trait value increased de-

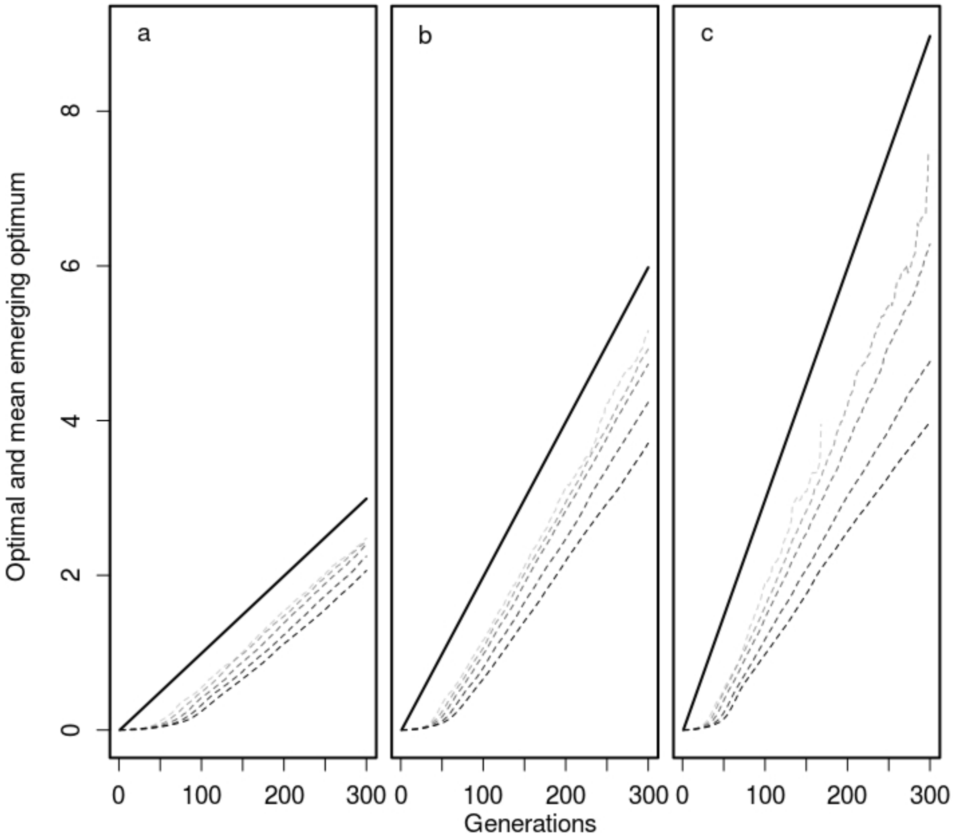

Figure 5.3: Emerging mean trait value of the individual optimum $\bar{h}$ for five values of trade-off strength $\alpha \in 1, 1.5, 2, 3, 4$(dashed lines) in the mean trend scenarios over time. Different shades of gray indicate a different trade-off strength: the lighter the gray, the stronger the trade-off. Low values of α indicate a stronger trade-off. Each panel is for one of the three : a) $\delta(\bar{H}) = 0.01$, b) $\delta(\bar{H}) = 0.02$ and c) $\delta(\bar{H}) = 0.03$.

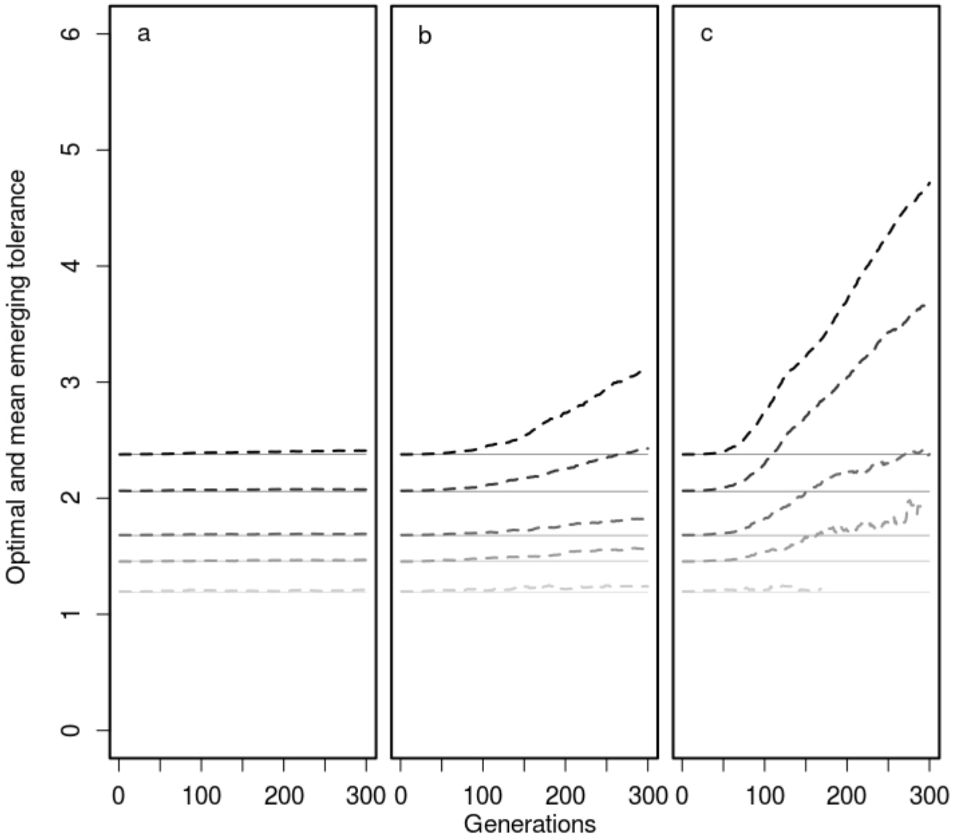

Figure 5.4: Mean trait value of the individual tolerance $\bar{g}$ for five trade-off strengths $\alpha \in 1, 1.5, 2, 3, 4$ (dashed lines) in the mean trend scenarios over time. Different shades of gray indicate different trade-off strength: the lighter the gray, the stronger the trade-off. Low values of α indicate a strong trade-off. a) $\delta(\bar{H}) = 0.01$, b) $\delta(\bar{H}) = 0.02$ and c) $\delta(\bar{H}) = 0.03$. The solid lines represent the numerical optimum $\hat{g}$ under stable habitat conditions (see Supplement 1) for the different values of α.

pendent on the trade-off strength. Niche widened for all but the strongest trade-off, where most populations soon went extinct. Thus all populations, except when the trade-off was very strong, could 'track' the development of the optimal tolerance trait value, even though an adaptation gap developed just as in the scenarios with an increase in mean (5.5). However, populations with a strong to intermediate trade-off went extinct, before the last simulated generation (300). In the last set of scenarios, the mean and the standard deviation were both increased, with the same annual increments (0.01, 0.02, 0.03). The emerging trait values of the optimum trait and the tolerance trait were similar to the previous scenarios with only an increase in standard deviation and are therefore not shown here.
With the rules for calculating of the optimal values of the tolerance trait one can also find a threshold value for the environmental standard deviation where the expected long-term geometric mean falls below 1 even with the best possible value for tolerance; beyond this value population growth becomes impossible and extinction is thus inevitable. An interactive version of the population development and trait evolution can be explored on: *theoreticalevolutionaryecologywuerzburg.shinyapps.io/therealpainofclimatechange/*.

5.5 Discussion

Our simulations demonstrate that different ecological and evolutionary responses to environmental change are possible, which may or may not result in ultimate extinction. Populations reach ecological and evolutionary equilibrium in both, the burn-in-periods and the control scenarios with emerging trait values of optimum h_i and tolerance g_i evolving as expected. The influence of an increasing mean and an increasing variance of the environmental parameter on the longevity of populations is obvious. For slow increases in the environmental mean, populations can continuously adapt the niche optimum without symptoms of "genetic exhaustion", no matter how strong the constraint on the evolution of higher tolerance is, similar to findings of Vincenzi (2014). The same can be found with an intermediate increase in mean environment, given the trade-off between tolerance and maximum number of offspring at the optimum is as well intermediate. When the trade-off is too pronounced, populations go extinct. When either the environmental standard deviation alone or both the sd and the mean increase over time, survival is only possible if the increase is slow and the trade-off is low to intermediate. When either the increase is too fast or the trade-off strength is too pronounced, populations go extinct

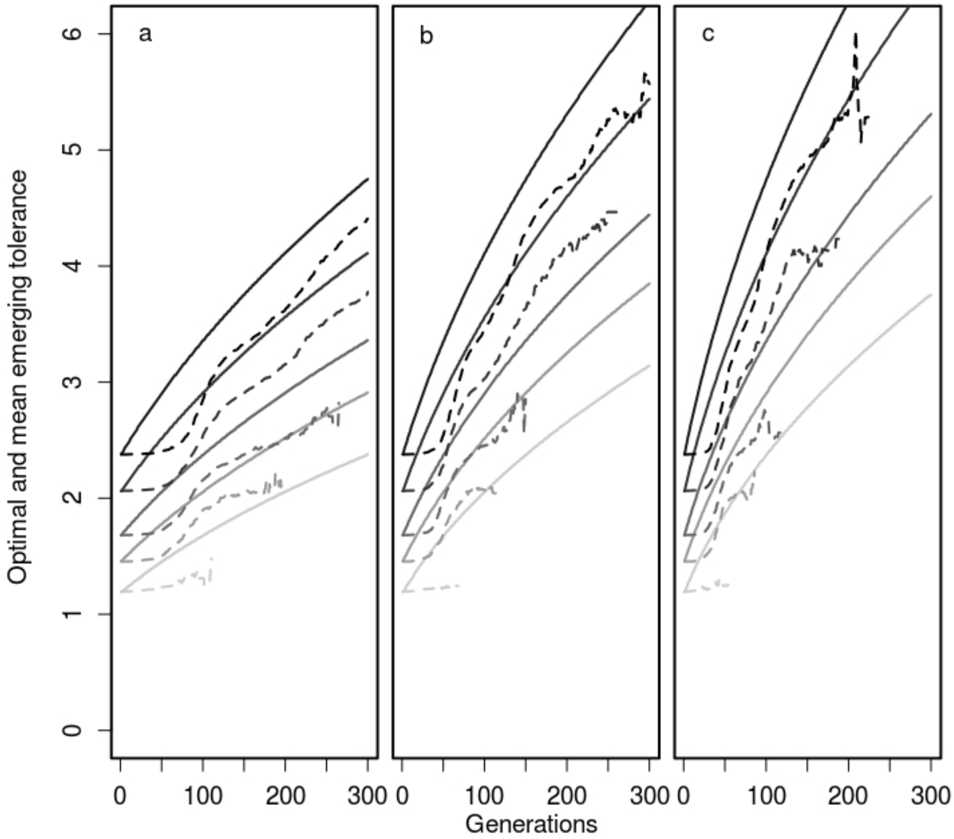

Figure 5.5: Mean trait value of the individual tolerance $\bar{g}$ for five trade-off strengths $\alpha \in 1, 1.5, 2, 3, 4$ (dashed lines) in the standard deviation trend scenarios over time. Different shades of gray indicate different trade-off strength: the lighter the gray, the stronger the trade-off. Low values of α indicate a strong trade-off. a) $\delta(\sigma_H) = 0.01$, b) $\delta(\sigma_H) = 0.02$ and c) $\delta(\sigma_H) = 0.03$. The solid lines represent the numerical optimum $\hat{g}$ under stable habitat conditions (see Supplement 1) for the different values of α.

before reaching the last simulated generation. Our first hypothesis can therefore be accepted. Only if the trade-off imposed on the population is too pronounced, the average niche is so narrow, that even the smallest annual increase cannot be tracked by evolution. Therefore the environmental change needs to be considered too fast for those populations, which again was part of the first hypothesis. The emerging adaptation gap is inevitable, since the selection for an increase in individual optimum works only on the current generation and cannot anticipate future developments. This is also the case in the scenarios with a fast increase in mean and a strong trade-off between stress tolerance and maximum number of offspring. In those scenarios only populations with an intermediate trade-off strength can track the environmental mean. Surprisingly in the scenarios with fast increase in mean but with a weak trade-off, the adaptation gap becomes continuously larger over time without population extinction (Fig 5.3c). This is possible because the individuals also increase their tolerance even beyond values that are optimal under no-trend conditions (Fig. **??**c). However, this results in declining population sizes, because the evolving high tolerance decreases the overall number of offspring, because of the trade-off imposed. A possible reason for this effect may be that selection on the optimum trait is always weak if tolerance is (already) large and further weakens once tolerance becomes bigger: Generally, selection on the optimum gets weaker as the tolerance gets larger. Additionally, in all scenarios the emergence of better adapted mutations can be a limiting factor, since the chance for a new mutation declines as population size decreases (Griffen and Drake 2008; Kawecki 2008; Schiffers et al. 2014). Note that the absolute probability of a mutation occurring, and thus a chance for a beneficial mutation occurring, is limited by the product of the population size and the mutation probability. However, we also simulated different mutation regimes (data not shown, but also see sensitivity analysis in S3), leading to higher genetic diversity, and still the same patterns emerged.

Typically, we know little about possible limitations to mutation events and (the speed of) adaptation. However, the potential of a species to adapt to different conditions can in part be assessed by substituting space for time, when different populations of the same species are locally adapted to the environmental conditions they experience, e.g. in *D. melanogaster* (Bozinovic et al. 2011) or in *A. thaliana* (Fournier-Level et al. 2011; J. F. Scheepens et al. 2018b). In both species, the thermal optimum of populations usually adapts to local conditions.

When the environmental standard deviation of the environmental parameter increase, extinction would ultimately be inevitable (that is, if the trend continues too long), no matter the speed of the increase, even though the populations adapt by increasing the tolerance and the optimum. This is because a principal limit exists for the evolution of an ever larger tolerance, whenever a trade-off between tolerance and the maximum number of offspring at optimal conditions exists (see supplementary information S1); at some point there is no evolutionary strategy that allows long-term positive population growth. With both increasing trade-off strength or increasing individual tolerance, the maximum possible number of offspring decreases and equilibrium population size declines, as can be seen in the control scenarios. Nevertheless, when the annual increase in environmental standard deviation is small enough and the trade-off is weak, adaptation to the changing environmental conditions is possible over considerable periods through an increased tolerance, consistent with our second hypothesis. The emerging trait values match the numerically predicted values, even though the evolution of those values lags behind the optimal trait values by an adaptation gap similar to that observed for the evolving optimum trait. Extinction does not occur at the exact same time in the simulations as predicted by the numerical analysis (there defined by the moment the geometric growth falls below one) for three reasons: (i), stochastic effects determine the environmental parameter value as well as the mutation size and the initial genotypic variability, (ii), stochastic extinction when populations become small and (iii) the number of mutations in the populations declines as populations shrink, possibly leading, in a positive feedback effect, to an increasing adaptation gap (Kawecki 2008; Schiffers et al. 2014). A larger adaptation gap will itself contribute to earlier extinction as populations are not optimally adapted to current conditions.

The great importance of changing environmental variance has been found in an empirical study of Bartheld et al. (2017). They showed that the individual (short-term) fitness of tadpoles was more affected by an increase in variance of water temperature than an increase in mean water temperature. This is also corroborated by the results of the predicted ability from the linear model to reach the maximum number of generations: While an increase in mean of 0.03 per generation still allows for a survival probability of 0.1, the same survival probability can only be maintained if the increase in standard deviation is as low as 0.015. It is thus important to recognize that an increasing mean may forever (within fundamental physiological limits) be evolutionarily tracked, an increasing variance can never be tracked indefinitely if a certain trade-off as assumed here exists.

The congruence of the simulated environmental change with predictions from climate change scenarios or historical data strongly depends on the spatial scale and the environmental parameter in question. When considering temperature, all three simulated annual step sizes in temperature mean match climate change predictions or historical data for mean temperature. Scherrer et al. (2005) found an annual increase in mean temperature of 0.02 in the 30 year period from 1975 to 2004, which corresponds to the intermediate mean change scenario simulated here. The IPCC scenarios RCP 4.5 and RCP 8.5 also predict changes in mean temperature similar to the simulated ones (Alexeeff et al. 2018; IPCC 2014). However, the simulated increase in environmental standard deviation is not as consistent with the predicted and historical increase in temperature sd. Scherrer at al. (2005) as well as Sofaer et al. (2017) show that the dominant changes in temperature distribution are mainly an increase in mean and not in variability. However, when only assessing the increase in thermal variability during the summer months (June, July and August) in central Europe – the period where most insects and plants grow and reproduce -, the annual increase in temperature variance almost reaches the simulated scale (Crhová et al. 2018; Fischer and Schär 2008; Scherrer et al. 2005). Therefore, the scenarios with both an increase in mean and sd can be considered similar to the predicted changes in summer temperature. Further, climate change also affects precipitation and current predictions, indeed, forecast an increase in variability of rainfalls. Here the scale matches the simulated annual increases in sd more closely than for temperature (Sofaer et al. 2017), hence the scenarios with only an increase in sd match precipitation projections best. For other environmental parameters, the temporal scale of change could again be different and many parameters are additionally interlinked, e.g. precipitation, temperature and cloud cover influence soil humidity (Fischer and Schär 2008), which could be a very important environmental factor for the survival e.g. for plants.

The ecological effects and stress created by climatic changes may not necessarily be direct, e.g. heat stress, but may also come about by indirect effects where, for example, drought years affect the availability of critical resources. The generality of our model can help both empirical biologists and researchers interested in specific habitats to identify patterns in their data or to adjust their study parameters. To get a more interactive visualization of our findings, we implemented an online application for readers, which can be used as a tool to explore our model and the effects on population development and niche evolution (see theoreticalevolutionaryecologywuerzburg.

shinyapps.io/therealpainofclimatechange). The app can facilitate the exploration of e.g. experimental parameters when designing new empirical experiments to examine the influence of environmental change on populations, or for models exploring the extinction risk of both isolated populations and meta-populations.

The implemented a duration of climate change of 300 years can be object for reconsideration, since such a long period of change may seem unrealistic. It may indeed be unlikely that climate change (temperature and precipitation) will proceed linearly over a period of 300 years (another 250 year from now) – currently, we simply cannot know this and in particular whether measures to reduce emission of carbon dioxide and other climate relevant gases will be effective. Our simulations make clear however, that many populations may come under stress that may make populations more vulnerable to other changes like habitat change and fragmentation. Additionally, an increase in environmental variance leads already to an acute loss of fitness way before the extinction finally occurs (see supplementary figure S1); in our simulations extinctions occurred, depending on parameters, much earlier and within periods of climate change that can be considered realistic (Vincenzi 2014). Therefore the duration of climate change in our models, does not change the results regarding an increase in environmental variability, but help shed light on the survivability of an increase in environmental mean, even for prolonged periods of time. It is important to recognize that an increase in variance leading to selection for a broader niche will result in diminished fitness (geometric growth) of a species whenever a (relevant) trade-off as assumed in our model does exist. So, while the variance increase may be compensated by an adaptive response and reduce extinctions risks as compared to a population not showing such a response, the unavoidable decrease in fitness associated with such a response will make populations nonetheless more susceptible to other stressors and further add to the dangers imposed by climate change. In addition to local adaptation as simulated here, there are still other possible ways to deal with environmental change, which were not included in our model. It is possible for species to avoid adverse conditions altogether by dispersal in space and time (Bürger and Lynch 1995) . Dormancy or times of torpor could develop, when the conditions are only harsh in specific periods (Ellner and Shmida 1981). In particular, in heterogeneous landscapes moving individuals could also select to settle in other habitats that provide more suitable conditions for their phenotype under the actual climatic conditions. Such immigration of better adapted individuals could also save focal populations from extinction; in our simulations of just one population this effect is excluded. More permanently a range shift of the whole species may emerge, which is often observed as a way to overcome the difficulties posed to species by climate change (Chan et al. 2016; Cobben, Verboom, et al. 2012; Parmesan 2006; Schiffers et al. 2014). To investigate this further, the model should be expanded to the metapopulation level. Here, it would be of interest to investigate the influence of different dispersal strategies on the evolution of the ecological niche and population survival. Cobben et al. (2014) employed random dispersal as the means to shift the range, but they also stated that non-random (e.g. informed dispersal) could change the outcome of their model.

The number and fitness of offspring can also be influenced by maternal and epigenetic effects, which were not included in the model. Here, genetic and phenotypic variability depends only on the variability of the population at initialization and the mutation events. Further, our model system does not include sexual recombination, which could also affect trait variability and therefore evolution. However, for the analysis of the evolution of certain traits without interference of parental effects, asexual systems were deemed perfect by Drake and Griffen (2008). Vincenzi (2014) also showed that adaption to new environments is mostly dependent on the already existing genetic variance, which could diminish the importance of parental or epigenetic effects. Therefore, a haploid model without recombination can be considered fitting for our model system, especially, since the standing genetic variance in the population is considerable (10000 individuals, each with a distinct set of traits). Nevertheless, Proulx and Teotónio (2017) have shown that in environments were the parental environment is not informative about the offspring environment, randomizing maternal effects can increase fitness: By diversifying the offspring phenotype the overall fitness is higher, when a certain proportion of offspring has the phenotype best suited for the current environment. Such a bet-hedging strategy was found in sticklebacks, exposed to unpredictable environmental variability (Shama 2015, 2017). Maternal effects can also be the amount of care given to the offspring, which was found to increase the survival of mice (Gyekis et al. 2011). The influence of both the parental environment and the parental investment could be included in future models to explore their effect on the evolution of the ecological niche. Griffen and Drake (2008) also noted that species interactions should not be forgotten when assessing extinction risks, since community ecology can alter the effects of environmental factors. Species competing for resources, for example, could worsen the effects of the environmental change and lead to even earlier extinction, especially when prey species are also influenced directly by the environmental change. The model we present here only includes a stable annual increase in the standard deviation of the environmental parameter, but it was shown that climate change often leads to more frequent disturbances as well (Bailey and Pol 2016; Easterling et al. 2000). To the degree that the increase of weather extremes can be seen as an increase in the variance of the environment this is already included in our simulations. However, the problem may be more severe if the distribution of weather conditions would follow more fat-tailed distributions than the normal distribution as we or others (e.g. Scherrer et al. 2005; Vincenzi 2014) assumed. In this case very extreme events could completely eradicate populations as populations can hardly evolve strategies for coping with such events, especially when the species in question has a low number of offspring per generation (Vincenzi 2014). A high number of offspring, as implemented here, can save populations (Bürger and Lynch 1995; Griffen and Drake 2008), at least for a certain time (even though here changing the number of offspring did not significantly reduce the extinction risk, S3). Survival of such extreme events may, however, be associated with genetic bottlenecks, therefore decrease the genetic variability and make the population more susceptible to inbreeding depression and subsequent extreme events (Griffen and Drake 2008). Furthermore, we assume a constant trade-off strength for a whole population over the simulated time span. In contrast, Rutschmann et al. (2016) show that the trade-off shape itself can vary within years, depending on the environment. In ectotherms, an increase in mean temperature alleviates the trade-off strength between litter size and egg size. They argue that the higher mean temperature can lead to higher physiological activity and thus to higher efficiency in resource acquisition and digestion. This in turn can lead to females having sufficient energy to increase the number of offspring without producing smaller eggs. However, higher temperatures also lead to higher adult mortality, which could counteract the positive effect of warmer temperatures on fitness (Rutschmann et al. 2016).

The assumption of existing trade-offs is used widely (D. A. Roff and D. J. Fairbairn 2007), and can also be found in empirical data (e.g. J F Scheepens et al. 2018a). Without the assumption of trade-offs, species could evolve an indefinitely broad niche with identical fitness under any conditions (Romero-Mujalli et al. 2018; Schiffers et al. 2014). This would mean that there could be a species adapted to all conditions it can encounter, which would spread all over the world, making biodiversity obsolete. Since we do have different species, living in different, heterogeneous habitats where their fitness varies, it is safe to make this basic assumption. In the present simulation, the tolerance trait values of whole populations develop in the same direction, depending on the trade-off strength. Under a strong trade-off, the mean tolerance of the population is evidently smaller (more specialist), while under a weaker trade-off, the mean tolerance becomes larger. This is most pronounced, when the environmental variance increases, which was already shown by Cobben et al. (2012) who reported a high proportion of generalists in environments with a high variance and Vincenzi (2014) who showed that in highly stochastic environments, specialists have a higher risk of extinction compared to generalists. There, the genotype was made up of two distinct heritable alleles, in contrast to the present study, where the tolerance trait is continuous. Therefore, the trade-off and the resulting fitness (maximum number of offspring) also fall into a continuous spectrum.

Since one can assume that there are always constraints to the evolution of a broader niche, due to energy or resource allocation, any scenario with an increasing environmental variability imposes a fitness reduction. Many aspects of the influence of environmental variability on e.g. species' resilience to climate change or niche evolution in metapopulations, still need to be explored, but to actually tackle the challenges species face under climate change, environmental variance needs to be included in both theoretical and empirical research.

5.6 Acknowledgements

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Supplementary Information

Supplementary information 1: Optimal tolerance and corresponding fertility

The optimal habitat tolerance $\hat{g}_i$ for any values of σ_H and α of for all values α_j ($\alpha_j \in 1,1.5,2,3,4$) can be found numerically by estimating the long-term expected geometric mean fertility for any particular strategy g_i $F_G(g_i|\sigma_H,\alpha_j)$ by applying the following equations:

$$G(g_i|\sigma_H,\alpha_j)=\sum_{H_t=-\infty}^{H_t=\infty}[\ln(R_0\cdot s(g_i,H_t,\alpha_j))\cdot\Phi(H_t|0,\sigma_H)\cdot\Delta_H] \text{ and}$$

$$F_G(g_i,\alpha_j)=e^{G(g_i,\alpha_j)}$$

where $\Phi(H_t|0,\sigma_H)$ is the probability that the habitat attribute takes the value H_t and $s(H_t,g_i,\alpha_j)$ is the expected number of offspring for an individual following strategy g_i given a trade-off parameter of α_j and habitat condition H_t. We then identify the value $\hat{g}_i$ that provides the maximum value for F_g (Fig S1a). At the same time we can also identify the limits of existence by identifying combinations of σ_H and α_j that generate values of $F_G(\hat{g}_i|\sigma_H,\alpha_j)\leq 1$.

To do so, the expected survival $s(H_t,g_i)$ for genotypes with $h_i=0$ and g_i between 0.1 and 8 in steps of 0.01 and a standard normal distribution of H_t with mean $\bar{H}=0$ and standard deviation σ_H between 1 and 10 in steps of 0.01 was calculated. Afterwards the geometric mean of the survival and its probability density across the space of H_t was determined. Only when the expected fitness is larger or equal to 1, i.e. one offspring per individual with an R_0 of 10, the genotype survives. The optimal value $\hat{g}_i$ is determined by a maximum expected fitness (Fig S1b).

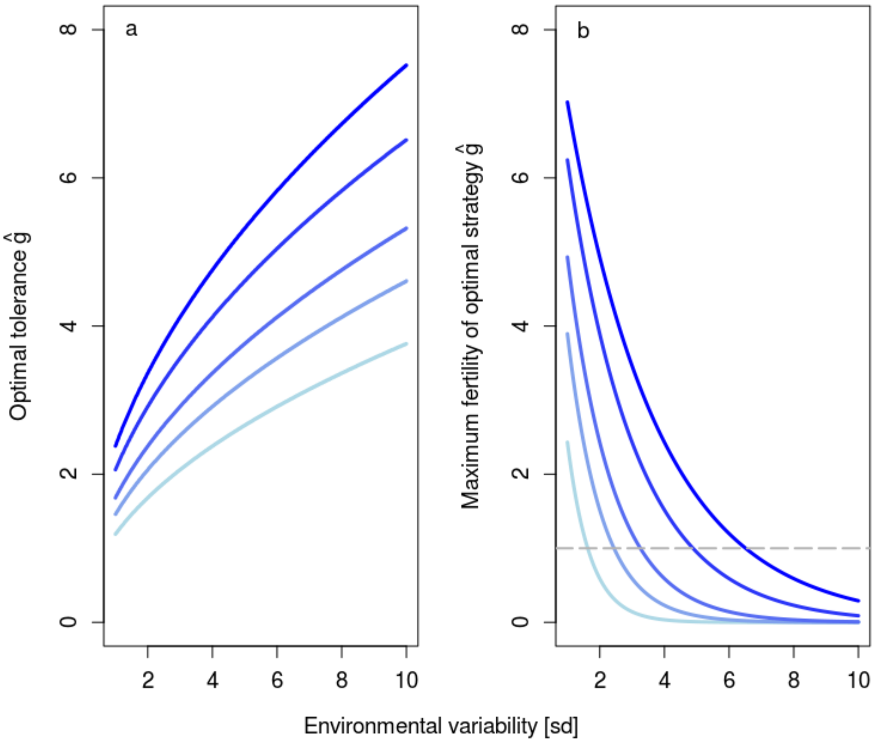

Figure S 1: Numerically determined optimum tolerance $\hat{g}$ *(a) and the corresponding maximum fertility (b) for values of* σ_H *between 1 and 10 and five different trade-off strengths* $\alpha \in (1, 1.5, 2, 3, 4)$. *The lighter the blue, the stronger the trade-off (smaller* α *). The grey line in panel (b) indicates limiting fertility of one offspring per individual while optimally adapted.*

Supplementary information 2: maximum number of offspring for certain tolerance values

The maximum number of offspring possible for individuals adapted to the environmental mean and with a given tolerance trait value can also be determined, by the fitness function:

$S(H_t, g_i) = R_0 \cdot T_h \cdot e^{\frac{-(H_t - h_i)^2}{g_i^2}}$ with

$T_h = e^{\frac{-g_i^2}{2\alpha^2}}$ and $H_t - h_i = 0$ (Fig S2).

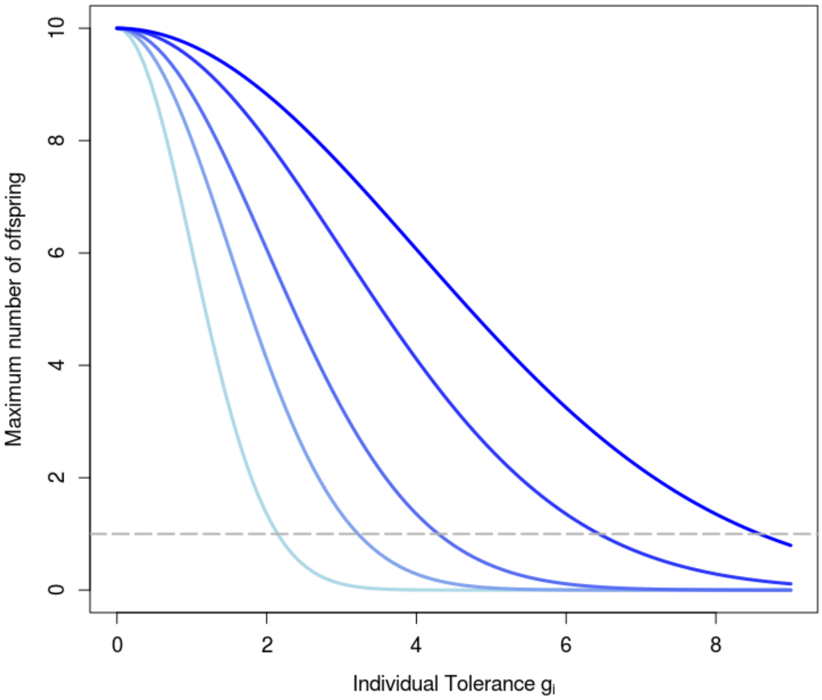

Figure S 2: Maximum possible number of offspring for individuals perfectly adapted to the environmental mean for values of g_i *between 0.1 and 9. The grey lines indicates the limiting number of offspring per individual (1)*

Supplementary information 3: sensitivity analysis of the parameter space

We performed a sensitivity analysis to explore whether the simulation outcome changes with a different set of parameter values. For this we changed the parameters of interest in scenarios with an intermediate trade-off strength (α =2) and intermediate annual increases $\delta(\bar{H})=\delta(\sigma_H)=0.02$. The parameters of interest are R_0, the mutation probability, and the mutation amplitude. The mutation amplitude is given as multiples of the trait value standard deviation: If the mutation amplitude is 0.5, the parental trait value can change by up to 0.5 standard deviations of the initial trait distribution. Neither an increase nor a decrease in fecundity R_0 changed the qualitative outcomes of the different climate change scenarios, as was the case for mutation probability and mutation amplitude.

Table 1: Parameter combinations for the sensitivity analysis and qualitative outcome of the simulations Mutation amplitude is given in multiples of the standard deviation of the initial trait distribution.

α	R_0	mutation probability	mutation amplitude	increase in mean	increase in sd	extinction time
2	5	0.001	0.5	0.0	0.0	300
2	5	0.001	0.5	0.02	0.0	300
2	5	0.001	0.5	0.0	0.02	81
2	5	0.001	0.5	0.02	0.02	63
2	15	0.001	0.5	0.0	0.0	300
2	15	0.001	0.5	0.02	0.0	300
2	15	0.001	0.5	0.0	0.02	151
2	15	0.001	0.5	0.02	0.02	144
2	10	0.01	0.5	0.0	0.0	300
2	10	0.01	0.5	0.02	0.0	300
2	10	0.01	0.5	0.0	0.02	115
2	10	0.01	0.5	0.02	0.02	105
2	10	0.0001	0.5	0.0	0.0	300
2	10	0.0001	0.5	0.02	0.0	300
2	10	0.0001	0.5	0.0	0.02	89
2	10	0.0001	0.5	0.02	0.02	124
2	10	0.001	0.1	0.0	0.0	30
2	10	0.001	0.1	0.02	0.0	300

2	10	0.001	0.1	0.0	0.02	181
2	10	0.001	0.1	0.02	0.02	124
2	10	0.001	1.0	0.0	0.0	300
2	10	0.001	1.0	0.02	0.0	300
2	10	0.001	1.0	0.0	0.02	51
2	10	0.001	1.0	0.02	0.02	116

6 | The degree of spatial variation relative to temporal variation influences evolution of dispersal

Since the second aspect of interest was the influence of spatial variation, we started working at a metapopulation level. We explored the evolution of the environmental niche, as we did before. However, we included several populations that were interconnected via random global dispersal and inhabited landscapes with varying spatial variation. We were particularly interested in the differences between average and extreme habitats.
This chapter was accepted by *Oikos* in July 2020.
I implemented the model, performed the analysis and drafted the manuscript. Thomas Hovestadt provided additional analysis and contributed to the manuscript. My overall contribution to this manuscript was 75%.

6.1 Abstract

In the face of ongoing global climate and land use change, organisms have multiple possibilities to cope with the modification of their environment. The two main possibilities are to either adapt locally or disperse to a more suitable habitat. The evolution of both local adaptation and dispersal interacts and can be influenced by the spatial and temporal variation (of e.g. temperature or precipitation). In an individual based model (IBM), we explore evolution of phenotypes in landscapes with varying degree of spatial relative to global temporal variation in order to examine its influence on the evolution of dispersal, niche optimum and niche width. The relationship between temporal and spatial variation did neither influence the evolution of local adaptation in the niche optimum nor of niche widths. Dispersal probability is highly influenced by the spatio-temporal relationship: with increasing spatial variation, dispersal probability decreases. Additionally, the shape of the distribution of the trait values over patch attributes switches from hump- to U-shaped. At low spatial variance more individuals emigrate from average habitats, at high spatial variance more from extreme habitats. The comparatively high dispersal probability in extreme patches of landscapes with a high spatial variation can be explained by evolutionary succession of two kinds of adaptive response. Early in the simulations, extreme patches in landscapes with a high spatial variability act as sink habitats, where population persistence depends on highly dispersive individuals with a wide niche. With ongoing evolution, local adaptation of the remaining individuals takes over, but simultaneously a possible bet-hedging strategy promotes higher dispersal probabilities in those habitats. Here, in generations that experience extreme shifts from the temporal mean of the patch attribute, the expected fitness becomes higher for dispersing individuals than for philopatric individuals. This means that under certain circumstances, both local adaptation and high dispersal probability can be selected for for coping with the projected environmental changes in the future.

6.2 Introduction

In the face of ongoing global climate and land use change, organisms have multiple possibilities to cope with the modification of their environment. The two main possibilities are to either adapt locally or disperse from their original, increasingly unsuitable habitat to more suitable habitats (Barnes et al. 2015; Bowler and Benton 2005; Fournier-Level et al. 2011; Hillaert et al. 2015; Hoffmann and Sgró 2011; Romero-Mujalli et al. 2018; Schiffers et al. 2014). Both strategies however, have their own set of constraints and evolutionary patterns.

Given a large enough intraspecific variation (Hoffmann and Sgró 2011; Sieger et al. 2019; Vincenzi 2014), high mutation rates or large mutation amplitudes (Schiffers et al. 2014) organisms can adapt rather quickly to a changing habitat by adjusting their niche optimum. Survival depends, however, also on the ability to cope with short-term temporal fluctuations of the environment and thus the innate specialist-generalist trade-off (Nguyen et al. 2019; Sieger et al. 2019; Vasseur et al. 2014; Vincenzi 2014). Together this leads to two general strategies, often described in the literature: specialists and generalists (Huey and Hertz 1984; Jacob, Laurent, Haegeman, et al. 2018). Specialists are described as organisms with a high fitness (e.g. reproductive success) at optimum conditions but a pronounced sensitivity towards deviations from that ideal environment, i.e. specialists have a narrow niche. Generalists have a broader niche and are therefore less susceptible to fluctuations in environmental conditions that deviate from their niche optimum, but at the same time, have a lower fitness at said optimum. The existence of such a trade-off was shown not only to be true when comparing different species (MacDonald et al. 2018), but also as part of intra-specific variation (Fournier-Level et al. 2011; J F Scheepens et al. 2018a). Tolerance to environmental conditions can also result from phenotypic plasticity, where organisms can change their own phenotype according to environment condition without loss of maximum fitness (Charmantier et al. 2008; DeWitt et al. 1998; Gunderson et al. 2017). In modeling contexts, both niche width and change of phenotype have been used to account for habitat tolerance. Both characteristics of a niche (position of the niche optimum and niche width) can evolve and help organisms to adapt to changing conditions if mutations in either are beneficial (Bennett Scott et al. 2019; Sieger et al. 2019). However, evolution of the niche width is presumably constrained by the strength of a specialist-generalist trade-off: If evolution of a broader niche is costly, organisms might ultimately not be able to evolve a broad enough niche to cope with the existing environmental variation (Sieger et al. 2019), and thus have to choose different strategies to survive changes, e.g. by following a bet-hedging reproductive strategy of having offspring with distinct properties to spread mortality risk or by distribute offspring over different habitats.

Most organisms are able to either disperse by themselves or via propagules, e.g. seeds. The evolution of dispersal is influenced by a number of circumstances such as intense local competition – especially among kin – inbreeding avoidance, and the exploitation of spatio-temporally variance in fitness expectations (Bowler and Benton 2005; Clobert et al. 2009; Kaemingk et al. 2019; Kubisch, Holt, et al. 2014; Mayer et al. 2019; Schwarzmueller et al. 2019). Obviously, dispersal implies the ability of organisms, even under stable (average) conditions, to spread to new habitats, exchange genes between patches, and increase inclusive fitness (Bowler and Benton 2005; Mortier et al. 2018). However, it can affect the survival of metapopulations both positively and negatively (Fobert et al. 2019; Jacob, Chaine, et al. 2019; Kisdi et al. 2020; Masier and Bonte 2020; T. Cronin et al. 2020). Due to the spread of genes between patches, maladaptations can spread as well as beneficial adaptations. Overall, high dispersal can lead to synchronized population dynamics due to the exchange of many individuals and thus increase the probability of parallel extinction events. Then again, if maladapted populations go extinct, dispersal helps repopulate empty habitat patches and again promote metapopulation persistence (Bowler and Benton 2005). These metapopulation dynamics can influence the advantages and penalties of dispersal itself, forming and eco-evolutionary feedback loop (Bowler and Benton 2005; Kubisch, Holt, et al. 2014), possibly leading to an evolution of dispersal propensity over time (Clobert et al. 2009; Kubisch, Degen, et al. 2013; Kubisch, Holt, et al. 2014). Currently, most research deems dispersal a factor promoting ecological generalisation, because it counteracts local adaptation as genotypes are rapidly exposed to different habitat conditions (Kisdi 2002; Mortier et al. 2018; Stevens et al. 2014). In the face of ongoing habitat variability and change, leaving the natal habitat and moving to a new one is also a possible strategy for overcoming the challenges of a changing environment (Ophelie Ronce et al. 2005), in particular if temporal variability in habitat conditions occurs at a different scale than spatial variation. How the latter aspect might influence the evolution of dispersal and the niche seems to be understudied, especially with regard to the relationship between the magnitude of spatial and temporal environmental variation.

Here, we developed an individual based mechanistic model of a metapopulation with evolving dispersal probability, niche optimum and niche width, to account for all the aspects called for by Romero-Mujalli et al. (2018) and partly combining the approaches of Schiffers et al (2014) and Hilleart et al (2015). The metapopulations inhabit a landscape with an approximately normal frequency distribution of habitat attributes in space that undergo global temporal environmental variability to include the effect of both spatial and temporal variability on local adaptation and dispersal. Our scenario thus implies that temporal variation like climatic variation takes place at a much larger spatial scale than spatial heterogeneity at the landscape scale. In particular, we want to examine the influence of habitat frequency on local adaptation and dispersal, contrast the effect of spatial and temporal variance on such adaptation and consider the role of a trade-off between maximum fitness and habitat tolerance.

We hypothesize that I) local adaptation in the niche optimum increases when spatial variation is larger than temporal variation, II) local adaptation in the niche width is constant over landscapes and depends mostly on the imposed specialist-generalist trade-off and the temporal variation, and III) higher dispersal emerges jointly with wider niches.

6.3 Material and Methods

6.3.1 Overview

For this study, we expanded the model of an isolated population of annual, haploid individuals already described in Sieger et al. (2019) to a metapopulation model using the programming language Julia (Bezanson et al. 2012). Each patch (grid-cell) is characterized by a certain average habitat attribute such that the landscape exhibits spatial variability in habitat features. These attributes can be interpreted as reflecting certain environmental conditions like temperature, but every other continuous environmental variable is just as likely (e.g.precipitation, soil nitrogen content, water oxygen content, pH, or salinity). However, temperature or precipitation would fit the pattern of larger scale temporal variation and smaller scale spatial heterogeneity best. Habitat attributes also vary in time. The temporal variation is synchronized over the whole landscape. We performed three time series of five landscapes for two specialist-generalist trade-off strengths. This will be explained in more detail below. Each habitat patch in the metapopulation houses one populations as described in the

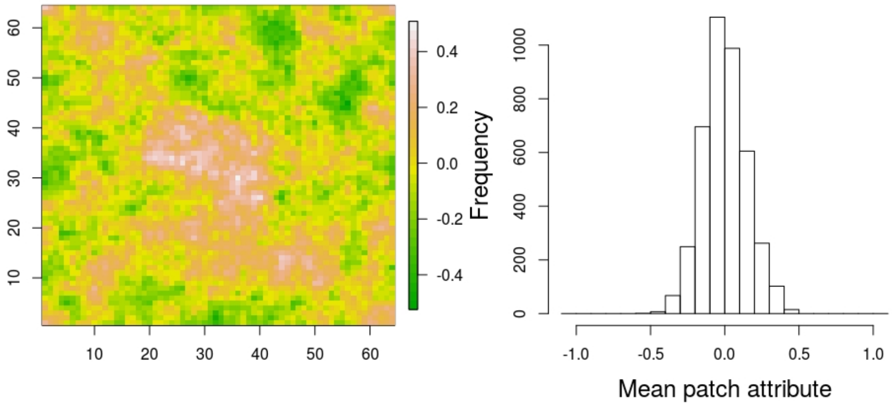

Figure 6.1: Example for landscape used in simulation experiments (for more details see text) with a standard deviation of 0.16. Because of the global dispersal assumed the arrangement of habitat patches is not relevant but only the frequency distribution of mean habitat attributes shown in the histogram.

above mentioned paper but individuals can also disperse to other patches by global dispersal. We use fertility (expected number of offspring) as a proxy for density-independent fitness: For each individual, fertility depends on the fit between an individual's niche optimum and current environment condition as well as the individual's niche width (see below). The dispersal trait and both niche traits are heritable and can mutate during inheritance thus allowing for adaptation to simulated conditions.

6.3.2 Landscapes

The metapopulation covers a spatially heterogeneous landscape of 64 by 64 habitat patches wrapped into a torus. We created five distinct landscapes using an algorithm for autocorrelated (fractal) landscapes with a Hurst-Index of 0.3, developed by Chipperfield et al. (2011). This algorithm generates an approximately normal distribution of habitat attributes. We standardized each generated landscapes to a mean of 0 by calculating the mean of the landscape and subtracting this mean from each patch's value. Because of the global dispersal assumed the arrangement of habitat patches is not relevant but only the frequency distribution of mean habitat attributes. Figure 6.1 exemplary shows one of the landscapes and the respective histogram for the distribution of environmental values. All five landscapes and their histograms can be found in the supplement (S1). The original landscapes had an average standard deviation of $\sigma_S = 0.32$ in the patches' mean habitat attribute.

In the simulation runs each landscape additionally experiences global temporal environmental variation: in every time step t a random value, drawn from a normal distribution with mean=0 and $\sigma_T = 1$, is added to any patch's mean environmental value to form the current environmental value of each patch. For repeatability and to avoid unaccounted variance we created three different time series of environmental variation, that are utilized in all of the simulation experiments described below. All following scenarios will thus be based on 5x3 replicated simulation runs.

Life-cycle and population dynamics.

Newborn adult individuals first disperse. Each individual has a heritable and mutable trait d that codes for the probability to leave its natal patch. An individual leaves the natal habitat, when a random number drawn from a uniform distribution $U[0..1]$ is lower than the individual's dispersal trait value. After this decision, an emigrating individual either dies with a given dispersal mortality ($m = 0.1$) or immigrates into a randomly selected new patch. Here, we only implemented global dispersal, since it is a common simplification in metapopulation models (Kisdi et al. 2020) to assume each individual can reach each patch in the metapopulation. After dispersal, density-independent but habitat dependent reproduction of the N_j adults i in each patch j takes place. The fit between environmental conditions and the individual i's niche, determines its reproductive success. If the niche optimum is not identical to the environmental value, the expected fertility is consequently lower then the maximum fertility under optimal conditions. As mentioned above, the individual's niche is defined by two heritable traits, the position of the niche optimum h_i in the environmental space and the niche width (tolerance) g_i. Combined, the two traits define a normal distribution for the expected fertility around the niche optimum. The number of offspring for each adult i is calculated, with inclusion of a generalist-specialist trade-off term, following Chaianunporn et al. 2015).

$$T_i = e^{\frac{-g_i^2}{2\alpha^2}} \tag{6.1}$$

Note that larger values of α imply lower trade-off costs. The resulting, environment dependent expected number of offspring for adult i with traits h_i and g_i in patch j, $L(H_{j,t}, g_i)$ at time t is calculated as:

$$L(H_{j,t}, h_i, g_i) = R_0 \cdot T_i \cdot e^{\frac{-(H_{j,t}-h_i)^2}{g_i^2}} \tag{6.2}$$

with R_0 the maximum possible offspring number. The actual number of offspring (larvae) born by each adult i in patch j is then generated by drawing from a Poisson-distribution with mean $L(H_{j,t}, h_i, g_i)$. When the difference between h_i and $H_{j,t}$ is low or the value of g_i is high, $L(H_{j,t}, g_i)$ is also high. The offspring inherit the three trait values from their parent, changed by a mutation event (see below). After the birth of all offspring, the adult population dies.

The total number of larvae $L(j,t)$ produced in patch j at time t then undergo density-dependent survival, with survival probability calculated according to the Beverton-Holt-model:

$$s_{i,j,t} = \frac{1}{1 + a \cdot L(H_{j,t}, g_i)} \tag{6.3}$$

with $a = \frac{R_0 - 1}{K \cdot R_0}$ and K the carrying capacity. This survival probability is used to allocate a random binomial factor to each individual offspring indicating whether it survives or not; the surviving larvae constitute the new adult population of the next generation. One time step t therefore equals one generation.

All three trait values of an individual are inherited from the parent and evolve by mutation and selection (see below). Evolution of the niche optimum and dispersal trait are not penalized, but according to equation (6.1) enlarging niche width underlies a trade-off of different strength (parameter α), depending on scenarios: It is either weak (i.e. evolution of a higher tolerance diminishes maximum fitness at the optimum only slightly), or strong, leading to a bigger drop in maximum fitness when tolerance increases. The traits of each individual mutate separately and in each generation according to the following rules. In principle, the niche optimum is not bound to a certain range. Therefore a value drawn from a normal distribution with mean 0 and standard deviation 0.03 is added to the niche optimum inherited from the parent. The tolerance trait value however needs to stay a positive number. Therefore a similar additive mutation (that might lead to adding negative values) is prohibited. Additionally, it seems sensible to scale the mutation amplitude to the parent values, to prevent too drastic changes. Therefore, the tolerance trait value inherited from the parent is multiplied with a value drawn from a uniform distribution between 0.97 and 1.03. The dispersal probability d is also changed additively by adding a value drawn from a normal distribution with mean 0 and standard deviation 0.001. Values for d can thus also take values outside the range [0 ..1] but this is not problematic, since the dispersal routine implemented treats dispersal with $d < 0$ as $d = 0$ and values of $d > 1$ as $d = 1$.

6.3.3 Initialization and scenarios.

All patches were initialized with 100 individuals each. Individuals were initialized with a niche optimum drawn from a normal distribution with mean 0 and standard deviation 1. The optimum is drawn from a normal distribution to start with a certain amount of variation, similar to the temporal variation. Since the optimum trait value and the environmental attribute can both have positive and negative values, drawing from both sides of zero seems sensible. The tolerance value however needs to be a positive value, to give the niche its shape. Therefore, the niche width (tolerance) was drawn from a Log-normal distribution with $sigma = 1$ and $mu = 0$. This avoids the emergence of negative values. The starting dispersal probability for each individual is 0.2. The single dispersal value was chosen to see the directional evolution of dispersal better. However, this does not limit the evolutionary potential of this trait, since we start with 409600 individuals in the very first generation, whose offspring all mutate in this trait. Therefore there is high evolutionary potential anyway.

The carrying capacity K of each patch is 1000 individuals, while the maximum number R_0 of offspring per individual is 10 (only when perfectly adapted to the environment).

To contrast the effect of spatial vs. temporal variation, we further created variations of the 5 landscapes by modulating the magnitude of spatial variation. In the original set of landscapes, the temporal and the spatial variation had standard deviations of $\sigma_T = 1$ and $\sigma_S = 0.32$ respectively. To achieve different relationships, we kept the temporal variation the same and multiplied each patch attribute in the landscapes with either 4 (spatial variation higher than temporal variation, $\sigma_S = 1.28$), 2 or 0.5 (spatial variation smaller than temporal variation, $\sigma_S = 0.64$ and 0.16). This leads to 20 distinct landscapes. A single simulation run was carried out over 200 time steps (=generations). For each landscape and each scenario simulations were replicated three times, using three different vectors of global temporal variation. Additionally, we performed exploratory simulations with different degrees of dispersal mortality and a weak trade-off strength. To look into the effect the dispersal mortality has on the evolution of the ecological niche and the dispersal probability, we performed one replication of one landscape for each degree of spatial heterogeneity with dispersal mortality $m = 0.0$ and $m = 0.2$.

6.3.4 Analysis.

Graphical presentations of results were created using R (Team 2018) with the 'tidyverse' package (Wickham et al. 2019). No statistical significance tests on the results were performed, since this is not meaningful in modeling approaches. For each patch in each landscape scenario the means of all trait values were calculated, as well as the mean population size and fertility (as a proxy for fitness) every fifth generation. A smooth curve was fitted to the data using the "gam" method of the geom_smooth function, which uses a generalized additive model for fitting. In each landscape, exemplary patches of the environmental average and extreme were examined to highlight the trait evolution over time. Here, the smooth curve was accomplished with the "loess" method of the plotting function. Additionally, the evolved individual trait values were recorded for a single patch with the same, arbitrarily chosen coordinates in each landscape for each simulation in the last generation. Out of those patches, the ones with patch attributes close to the landscape mean ('average') or far from the landscape mean ('extreme') were selected. Results from these patches were used as examples for the individuals' trait spaces in the respective patches. The resulting data is not shown here.

6.4 Results

Overall, the results did not differ qualitatively between trade-off strengths, therefore we only show the results for the weaker trade-off. The corresponding results for the stronger trade-off can be found in the supplementary material (S7 and S8). The outcome was also very similar for the different dispersal mortalities $m \in (0.0, 0.2)$ and are also not shown here but can be found in the supplementary material (S9)

6.4.1 Local adaptation in the environmental niche

The average niche optimum value of individuals in the last generation approximates the corresponding patch's mean environment (Fig. 6.2 a), showing a close relationship between the trait means and the patches' mean attribute values. This is consistent for both trade-off strengths. However, in particular with the weaker trade-off and when spatial variance is smaller or equal to the temporal variance, a tendency of a 'regression towards the mean' can be noticed with individuals in extreme habitat patches not exactly adapted to local conditions. The evolving mean niche width trait values in the last generation are only influenced by trade-off strength. In the scenarios with a stronger trade-off, niche width expectedly becomes narrower than in the scenarios with a weaker trade-off. In generation 200 (final time step) populations in all patches have established about similar mean niche widths independent of the patches' habitat attributes (see S2). However, the evolution of the niche width trait value over time differs with degree of spatial variation. With increasing spatial variation, the difference in temporal progression of niche width between central and extreme patches becomes more pronounced. In particular, with $\sigma_S : \sigma_T = 1.28 : 1$, in early generations, the average niche width trait values in extreme patches are much bigger than the average niche width trait values in average patches. The values for niche width also show much more variance in the extreme habitats. Over time, however, the niche width trait values in extreme patches approach the values in average patches (Fig. 6.3 a), leading to the homogeneous trait distribution over patch mean attribute described above.

6.4.2 Evolution of dispersal

The patch-wise mean dispersal probability in the last generation decreases with increasing spatial variation for both implemented trade-off strengths; the strength of the trade-off itself has little effect on dispersal evolution. We also recognize a larger across patch variability in the mean dispersal trait with larger spatial variance (Fig. **??**). Furthermore, the distribution of the mean trait values over the patches' environmental mean value changes from hump shaped when $\sigma_S < \sigma_T$ (spatial variation lower than temporal variation) to U-shaped when $\sigma_S > \sigma_T$ the same pattern shows when plotting the patch-wise mean dispersal trait values of individuals over their mean evolved local niche optimum (Fig. **??** b)). Indeed, the largest mean dispersal traits across all scenarios are observed in extreme habitat patches in scenarios with the largest spatial variance, despite the fact the we also see evolution of the lowest mean dispersal in average patches for those same scenarios. Following initialization dispersal probability decreases over time in all scenarios but a stable difference establishes between the average and the extreme habitat patches in the landscapes with the highest spatial variation (Fig. 6.3 b)

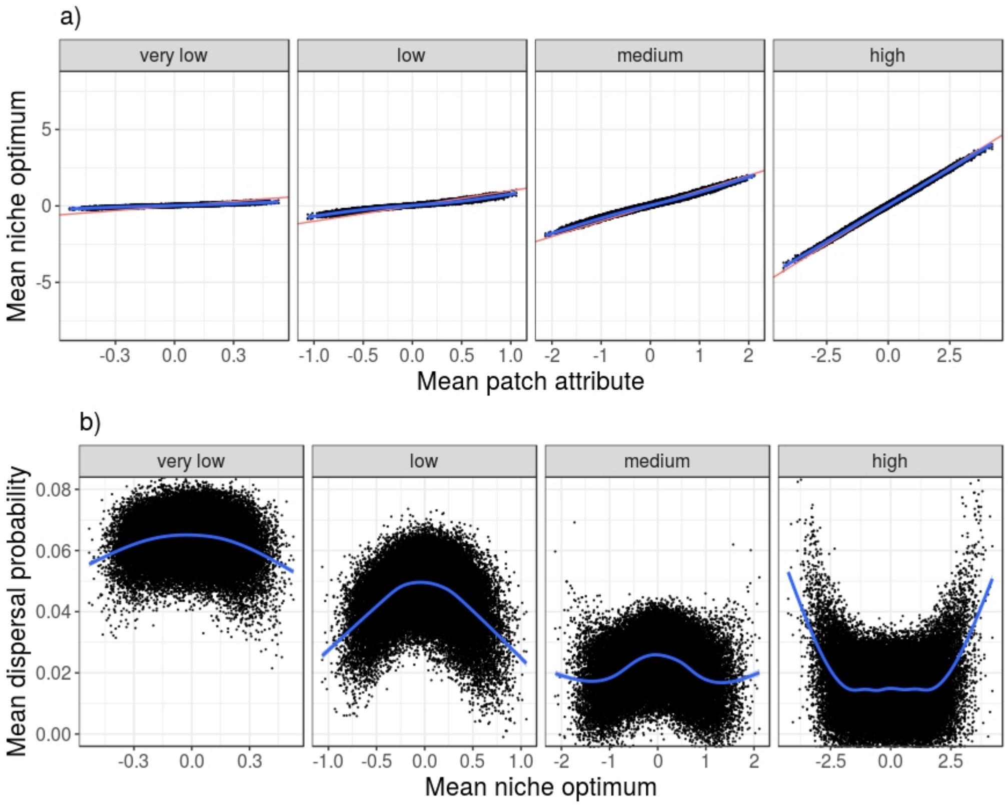

Figure 6.2: a) Mean niche optimum trait value calculated in the last generation for each patch plotted over the patches' mean environmental attribute H_j. Panels show values for four degrees of spatial variation, which increases from left to right and is labeled relative to the temporal variation of $\sigma_T = 1$. Mean niche optimum trait values (fitted blue line) approximate the patches' mean environmental attribute (red line) indicating local adaptation. b) Mean dispersal trait value of each patch plotted over the mean niche optimum trait value of the respective patch evolving by the end of the simulation. Data points from pooled data from the 15 replicate simulation runs for each scenario. Arrangement and classification of panels as in panel a).

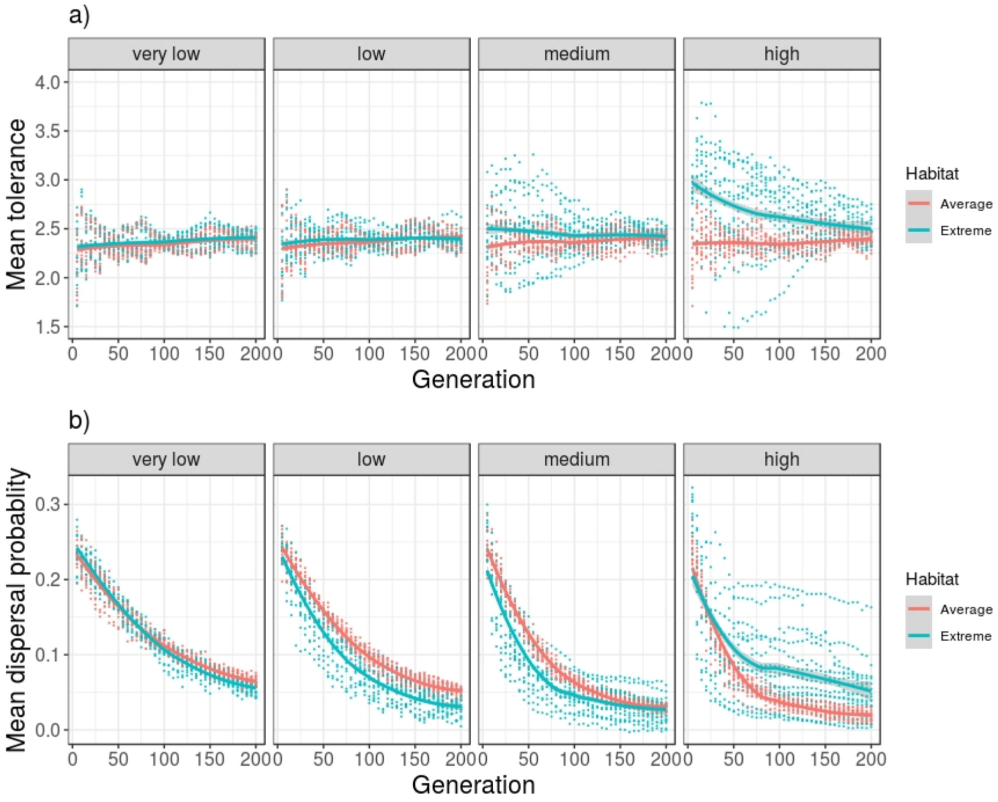

Figure 6.3: a) Evolution of patch-wise mean tolerance values over time, starting in the fifth generation for two patches per landscape. For each of the 15 replicate simulation runs (5 landscapes x 3 time series) the patch with the most extreme habitat (the patch with the highest absolute value for the habitat attribute; blue dots and line) and the patch closest to average conditions (the patch with the lowest absolute value for the habitat attribute; red dots and line) are shown. b) Change in patch-wise mean dispersal probability trait values over time, starting in the fifth generation for average (blue dots and lines) and extreme habitats (red dots and lines). Arrangement and classification of panels as in Fig. **??**

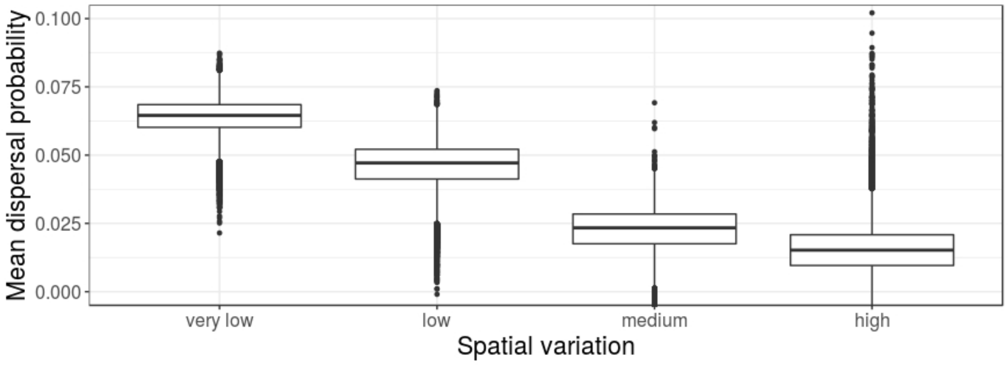

Figure 6.4: Box-plot of mean evolved dispersal traits values (averaged over 15 replicate scenarios) for the different degrees of spatial variation. Spatial variation increases to the right and is labeled relative to the temporal variation of 1.

6.4.3 Population size and fitness

To better understand the reasons underlying the larger dispersal probability evolving in more extreme habitats we analyzed the fitness (expectation) of the individuals in each patch by calculating the geometric mean of the expected fertility (as a proxy for fitness) of each patch over the whole simulation run. In landscapes with a spatial variation smaller than the temporal variation, the geometric mean of expected fertility of the patches stays constant over the whole spectrum of the patch environmental attributes. A stronger trade-off leads to an lower overall fitness. In landscapes with a spatial variation with sd 1.28, the geometric mean fertility becomes hump-shaped over the environmental spectrum. In more extreme patches the geometric mean of the expected fertility is smaller than in patches with an environmental attribute close to the landscapes mean (Fig. **??** b)). This hump-shape is found for both trade-off strengths.
Additionally, only in the geometric mean of the expected fertility there is a visible effect of the three different time-series used for the global temporal variance. The lowest fitness corresponds to the iteration, where the vector of values for temporal variation has the biggest range of values (= higher temporal variation, supplementary material, S3). This influence of the different time runs of temporal variation is consistent for all trade-off strengths. It is not found in the trait values, which are similar across all iterations and therefore similar across all time runs of temporal variation.

6.5 Discussion

6.5.1 Overview

Our simulations produce some expected results but also some unforeseen results that can be traced to the particular assumptions we make in our approach. We believe that our assumption of synchronized global temporal variance affecting a spatially structured landscape reflects a plausible scenario for some real world situations – in particular for the effects of climatic variation. The spatial variation experienced by any type of organism depends on the size of its 'daily activity range' and spatial demands on the one hand and its dispersal abilities on the other. For many organisms the former may only cover a few square meters and the latter distances of a few meters to a few kilometers – both scales, at which natural environments may show (strong) spatial variation in critical habitat attributes

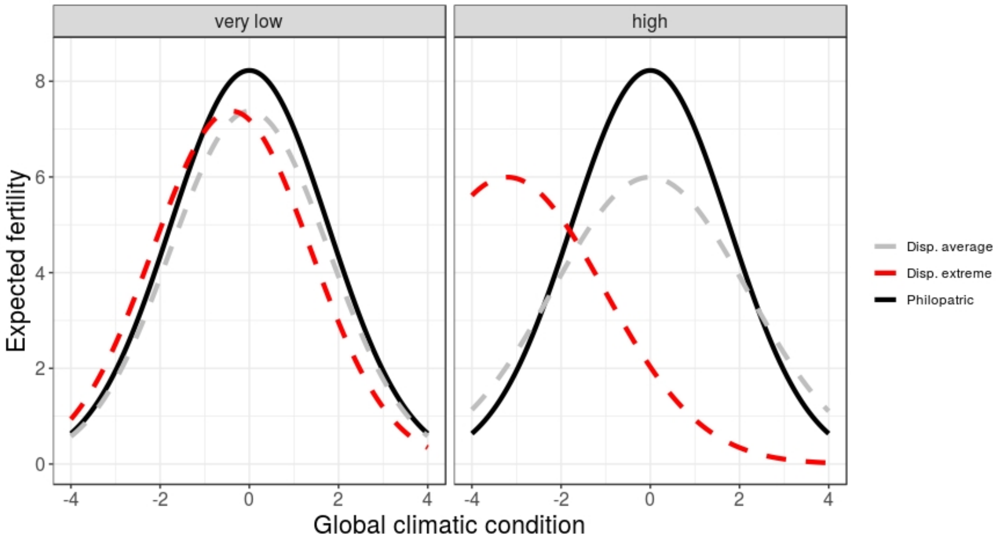

Figure 6.5: Expected mean fertility for individuals either remaining philopatric and adapted to the patch of origin ($h_i = H_j$) in dependence of actual climatic condition (black line) or randomly dispersing (accounting for 10% dispersal mortality). Grey hatched line for individuals adapted to and emigrating from an average patch ($H_j = 0$) and red hatched line for individuals adapted to conditions -2.5 spatial standard deviations below the spatial mean (cold adapted). Left panel shows values for the lowest spatial variation ($\sigma_S = 0.16$), the right column for the highest spatial variation ($\sigma_S = 1.28$).

including temperature or soil humidity. However, climatic conditions and year-to-year variance in such conditions tend to correlate over much larger distances so that even moving and dispersing individuals are not likely to experience different climate than those that do not disperse. Most interestingly, we observe an inversion in evolving emigration probability with increasing spatial habitat heterogeneity: at low spatial variance individuals were more likely to emigrate from abundant average habitats, whereas with high variance they emigrated with larger probability from rare but extreme habitats. Nonetheless, local populations were mostly adapted to the attributes of the patch of residence with equal habitat niche width evolving in average and extreme habitats. In the following, we will provide a more detailed discussion of these results.

6.5.2 Local adaptation.

Spatial heterogeneity will generally select for local adaptation and for lower dispersal as heterogeneity implies the cost of immigrating into non-suitable habitat (Mortier et al. 2018) and because dispersal has the tendency to generate a net-flow from large to small populations resulting in a net fitness-loss for dispersers (Hastings 1983; Venable and J. S. Brown 1993). In our simulation individuals' traits indeed tend to match, on average, the attribute of the patch of residence. In the scenarios with larger spatial than temporal variance mean niche optimum matched the patches' attributes so closely that individuals need to be considered perfectly locally adapted. However, for the scenarios with low spatial variance populations in extreme patches showed a relatively large degree of local maladaptation; this can certainly be traced to the net-gene flow from the abundant average habitats to the rare extreme habitats creating a 'regression towards the mean' effect. We must recognize, however, that this maladaption (gap) is small in absolute terms and has little fitness consequences; due to the selection imposed by the temporal variance on niche width (tolerance) individuals can easily cope with the much smaller spatial variance.

These results correspond with many empirical findings. A large proportion of natural populations show local adaptation (Hereford 2009; Schiffers et al. 2014), but it was also found that gene swamping – immigration of locally less adapted individuals – can hinder complete local adaptation (Bachmann et al. 2020; Bridle et al. 2019; Kawecki 2008; Weiss-Lehman and Shaw 2020). In case of steep environmental gradients even small populations can undergo rapid evolution and adapt to local conditions (Cropp and Norbury 2019). Ants, for example, were reported to show local adaptation, even in marginal habitats at their northern range edge (Nguyen et al. 2019). Fire salamanders could also adapt to environmentally extreme habitats which were connected to core zones and did show a high genetic diversity (Sinai et al. 2019); similar results were found by Schiffers et al. (2014).

6.5.3 Tolerance

Contrary to our expectation the tolerance levels ultimately evolving were only influenced by the trade-off parameter α but did not depend on the amount of spatial variation. The mean tolerance values evolving were in fact close to the optimal tolerance values reported in our previous study for scenarios with only a single population; the unavoidable temporal variance in environmental conditions imposes selection for a specific tolerance value that maximizes the geometric mean fitness (Sieger et al. 2019), thus preventing an extreme "narrowing" of the habitat niche on local average habitat conditions. Further, tolerance did not evolve to different values in average as compared to extreme habitat patches. Together, our findings suggest that evolution of dispersal probability and tolerance can be decoupled, especially when looking at the evolution of tolerance trait values in landscapes with low spatial variation over time.

6.5.4 Evolution in time

Results revealed clear temporal evolutionary dynamics, in particular in scenarios with large spatial variation. The initial rise to very high tolerance values in extreme patches is a consequence of the initialization routine: individuals were randomly initialized with trait values for the niche optimum taken from the same distribution as the temporal variation. This means that in extreme patches in landscapes with a large spatial variation, the individuals' niche optimum initially matched local habitat conditions poorly in the extreme habitats resulting in low fertility and frequent population extinction. Therefore, individuals with a high tolerance and high dispersal probability were initially favored, similar to results by Hilleart et al. (2015). Indeed, in our previous publication (ibid.) we could already demonstrate that an initial evolutionary response to local maladaption as, for example, initiated by climate change, may also be niche widening beyond the optimum under static average conditions as such a response can also reduce the cost of maladaptation. Only when the niche optimum had adapted to new conditions did the tolerance values evolve back to the optimal values again.

6.5.5 Dispersal

In our simulations, the implemented dispersal strategy was global dispersal, i.e. dispersing individuals reach any patches in the landscape with equal probability. This is usually considered an antagonist for local adaptation (Ducros et al. 2020; Jacob, Laurent, Haegeman, et al. 2018) and leads to selection against dispersal in spatially heterogeneous landscapes. But even if costly, a minimum of dispersal (and thus gene-flow) is nearly universally selected for driven by the emerging kin structure (Hamilton and May 1977; Poethke, Pfenning, et al. 2007) and exploitation of emergent stochastic variability in population sizes (Comins et al. 1980; Poethke, Hovestadt, et al. 2003). Not surprisingly, in our simulations evolution of average (median) emigration probability was consequently determined by the degree of spatial variation. Emigration probability declined as spatial variation increased due to the enlarged risk of dispersing into non-suitable habitat. In contrast, the magnitude of the trade-off had no noticeable effect on the mean evolving dispersal probabilities. More interestingly, in landscapes with lower or equal spatial than temporal variation, populations in extreme patches evolved lower emigration probabilities than those in average habitats (hump-shaped pattern in Fig. 6.4) whereas the opposite was true in scenarios where spatial variance was larger than the temporal variance (U-shaped pattern). To understand this we have to realize that the landscape 'looks' different from the perspective of individuals adapted to average than from that of individuals adapted to more extreme habitats. With the normal distribution of habitat attributes implemented in our simulations the former individuals likely immigrate into habitats more or less similar to the one of origin whereas the latter are likely to immigrate into very different habitats. In fact, in the scenarios with small spatial vs. temporal variance migrants surviving dispersal and adapted to average habitats can expect the same fertility than individuals that do not emigrate (cf. Figure 6.5). This is not quite so for individuals adapted to extreme habitats explaining the evolution of reduced dispersal from such habitats. In any case, long-term geometric mean fitness is much more dominated by the temporal variance in these scenarios that cannot be avoided by dispersing.

However, with spatial variance getting larger the landscape offers an opportunity for bet-hedging on the effects of temporal variation. In particular, in extreme years with low fitness expectations in the (on average) optimal habitat, emigrants may have much higher fitness expectations than philopatric individuals (Figure 10). Whereas this effect is about symmetric (with regard to the direction of temporal extremes) and rather weak for individuals adapted to average conditions it is highly asymmetric for individuals adapted to extreme habitats favoring dispersal in the latter group; in some extreme years such individuals may find favorable conditions in far more patches than in the average seasons. Conversely, for individuals adapted to average conditions only few patches will offer optimal conditions in extreme years. It is important to recognize that in our scenarios, and in contrast to other studies implementing spatio-temporal variance, the fitness expectations of emigrants do not fluctuate randomly as compared to that of philopatric individuals; emigrants can expect high rewards in particularly in years were conditions in the natal patch are very poor. For this reason the bet-hedging benefit is more important for individuals adapted to extreme habitats promoting evolution of higher emigration probabilities in these patches. By analyzing individual trait combinations recorded for single patches we could verify that this was not due to gene-swamping of more dispersive but poorly adapted individuals from other patches. In comparison to results from patches that had a mean closer to the landscape's mean, the trait for emigration probability took generally larger values in extreme habitats but was not correlated with the level of maladaptation.

Apart from this direct benefit of bet-hedging a second effect may add to the evolution of higher emigration probability in extreme habitats. Individuals adapted to extreme conditions have no chance of avoiding the drastic effects of temporal extremes in the “wrong direction” (cf. Figure 5) presumably leading to more frequent local lineage/population extinction. For example, a cold-adapted individual adapted to conditions 3 s.d. below the landscape average, will have very low fitness expectations in a very hot season wherever it is, whereas for individuals adapted to average conditions favorable conditions will occur in some habitat patches in every season. Lineages/Populations adapted to extreme conditions will thus suffer occasional local and even global population collapses increasing the likelihood of local extinction, the emergence of tighter kin-structure, and the chance for recolonizing suitable habitats; all these effects are known to promote evolution of dispersal (Hamilton and May 1977; Leturque and Rousset 2002; Poethke, Hovestadt, et al. 2003; Poethke, Pfenning, et al. 2007; Ophélie Ronce et al. 2000). We think that this is a likely added effect and it deserves further attention in future developments of our approach.

6.5.6 Limitations

The presented model makes some general (and common) assumptions for sake of simplicity and computational effectiveness. Some of these assumptions have the potential to influence our results on the evolution of dispersal and the environmental niche. First, the assumption of large-scale and random dispersal is not found as ubiquitous in nature and a high number of different and not mutually exclusive dispersal types and strategies can be found (e.g. Bowler and Benton 2005; Ducros et al. 2020; Fobert et al. 2019; Jacob, Chaine, et al. 2019; Jacob, Laurent, Haegeman, et al. 2018; Kisdi et al. 2020; Schwarzmueller et al. 2019; T. Cronin et al. 2020. In particular in spatially autocorrelated landscapes more local dispersal may be a better strategy as it assures immigration into habitats more similar to the habitat of origin (cf. Hovestadt et al. 2001). In addition, habitat dependent emigration, habitat choice when settling and density dependent dispersal are all mechanisms worth of exploring with the particular scenario we have implemented here – we expect that with such 'smarter' dispersal strategies a greater diversity of niche and dispersal strategies may evolve in complex landscapes. Sexual recombination can also play an important role in the evolution of dispersal (Leidinger and Cabral 2020; Weiss-Lehman and Shaw 2020) allowing for faster evolution and recombination. Nevertheless, the high standing variation in the founding population here ensured that inter-individual variability was high and sufficient phenotypic variability was present in the meta-population. Additionally, the 'time' and 'energetic' costs associated with dispersal, i.e. the costs associated with developing specialised dispersal organs and tissues or the time taken to disperse as described by (Bonte et al. 2012), might also be of interest. It would be possible to include these e.g. by implementing a trade-off between resource allocation to either reproduction and dispersalas described in e.g. Burton et al. 2010; Guerra 2011; Matsumura and Miyatake 2018; Renault 2020; Saglam et al. 2008. However, dispersal costs are already included in our simulations via the penalization of dispersal by a mortality cost and especially the local maladaptedness of dispersers in the new habitat often enough resulting in the reduction of the number of offspring for dispersing individuals. Adding investment costs for dispersal would certainly result in selection for (even) lower emigration probabilities, but would, in our opinion, not change the general results we present here.

6.5.7 Conclusions

Our simulations document the importance of spatial and temporal variance in environmental attributes for the evolution of both the ecological niche and of dispersal. Importantly – and in difference to many previous studies – our scenarios assume that temporal variation occurs at a much larger scale than spatial variance which creates different selective pressures than under the assumption of uncorrelated temporal variance (Poethke, Hovestadt, et al. 2003; Travis 2001). Further, in our simulations we assume a normal distribution for the occurrence of habitat attributes in space resulting in a high frequency of average habitats and low frequency of extreme habitats. This has the consequence that in our simulations some patches may on average be the best suitable for an individual with a given niche, but that the identity of patches with optimal conditions nonetheless is dynamic in time. This allows and selects for the evolution of bet-hedging strategies in particular in lineages adapted to more extreme habitat conditions.

Notwithstanding the limitations of the presented work, our results thus suggest that the combination of spatial and large-scale temporal environmental variation may have specific effects on trait evolution. We conclude that the degree of spatial variation relative to the global temporal variation is highly relevant for the evolution of dispersal in habitats of different frequency but has only small effects on the evolution of niche attributes.

6.6 Acknowledgements

We would like to thank Juliano Sarmento Cabral and his working group as well as Joseph Tardanico for fruitful discussions. This project is funded by the German Research Foundation DFG, KU 3384-1/1.

Supplementary information to ”The degree of spatial variation relative to temporal variation influences evolution of dispersal”

C.S. Sieger and T. Hovestadt

2020

1 Landscapes

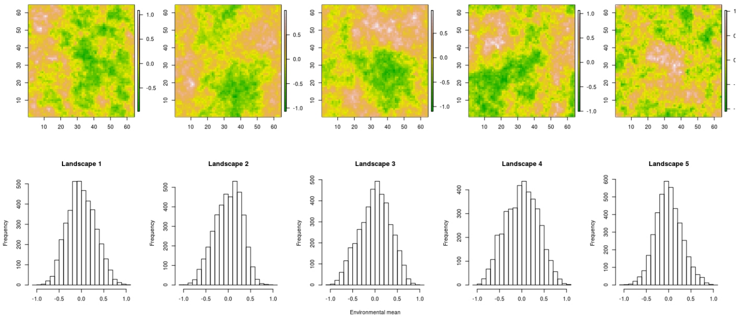

Figure S 1: The five different landscapes used in the simulations with the corresponding habitat frequency distributions (sd = 0.32). Landscapes with different sd were generated by multiplying each habitat attribute with a factor, so that the shape of the frequency distributions was not altered. The landscape shown in Figure 1 of the manuscript is landscape 5.

2 Tolerance trait values

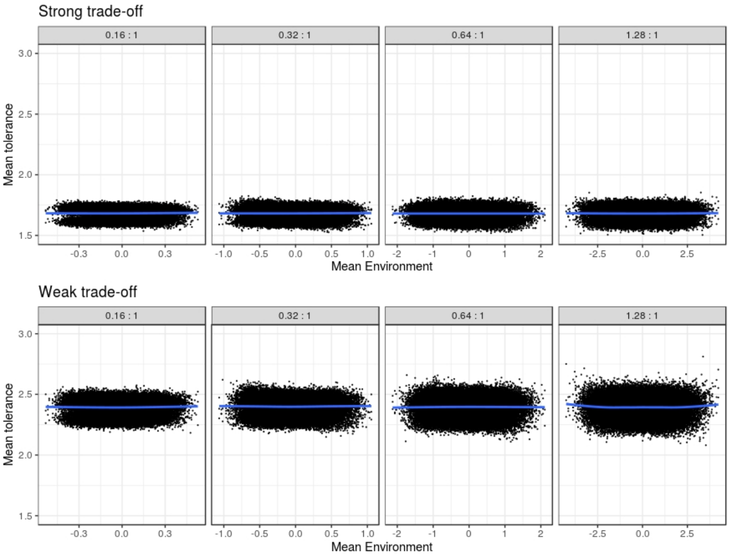

Figure S 2: Mean tolerance trait value calculated in the last generation for each patch plotted over the patches' mean H environmental attributes. Panels show values for four degrees of spatial variation (increasing from left to right) and two trade-off strengths (top row for strong, bottom row for weak trade-off). Spatial variation is labeled relative to the temporal variation of $H = 1$. No difference in trait values between degrees of spatial variation can be seen, but a quantitative difference between the trade-offs strenghts is visible. As expected, a stronger trade-off leads to the evolution of lower tolerances.

3 Temporal change

Three different time series for environmental fluctuations utilized in comibination with the five different landscapes to create the 15 replicate simulation runs for each scenario. As shown below, the second time run had the higher range of values and contained more extreme events then the other two iterations. This influenced the geometric mean fertility (see figure S 4).

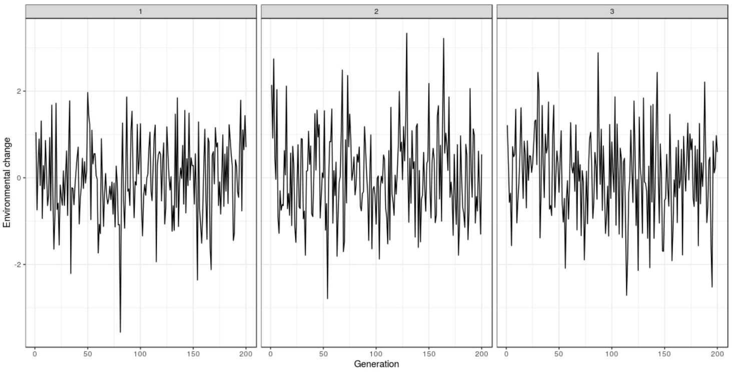

Figure S 3: The annual environmental change plotted over the respective generation it occured in, for three iterations.

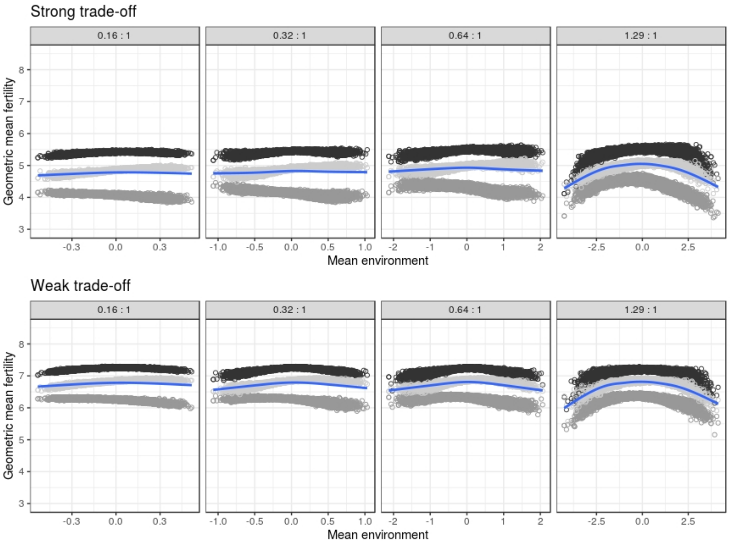

Figure S 4: Geometric mean fertility for populations in habitats of different attributes. Panels show combined data from all 15 replicate simulation runs. The influence of the three different temporal variation runs is clearly visible in the grey shading. The lowest fertility corresponds with iteration number 2 (dark grey) in figure S3.

4 Results for a strong trade-off

In the manuscript, we show only the results for a weak specialist-generalist trade-off, since the results for a strong trade-off are qualitatively the same. The following figures show the results for a strong trade-off, structured similarly to the figures in the manuscript.

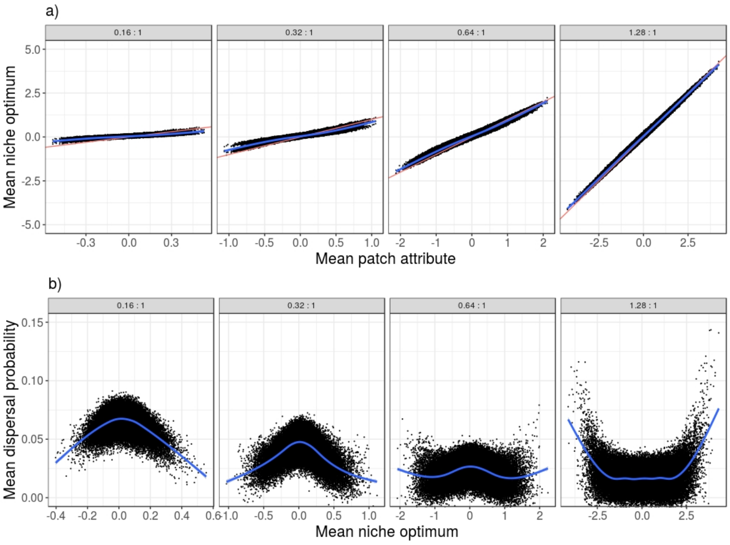

Figure S 5: a) Mean niche optimum trait value calculated in the last generation for each patch plotted over the patches' mean environmental attribute σ_S . Panels show values for four degrees of spatial variation, which increases from left to right and is labeled relative to the temporal variation of $\sigma_T = 1$. Mean niche optimum trait values (fitted blue line) approximate the patches' mean environmental attribute (red line). b) Mean dispersal trait value of each patch plotted over the mean niche optimum trait value of the respective patch evolving by the end of the simulation. Data points from pooled data from the 15 replicate simulation runs for each scenario. Arrangement and classification of panels as in panel a).

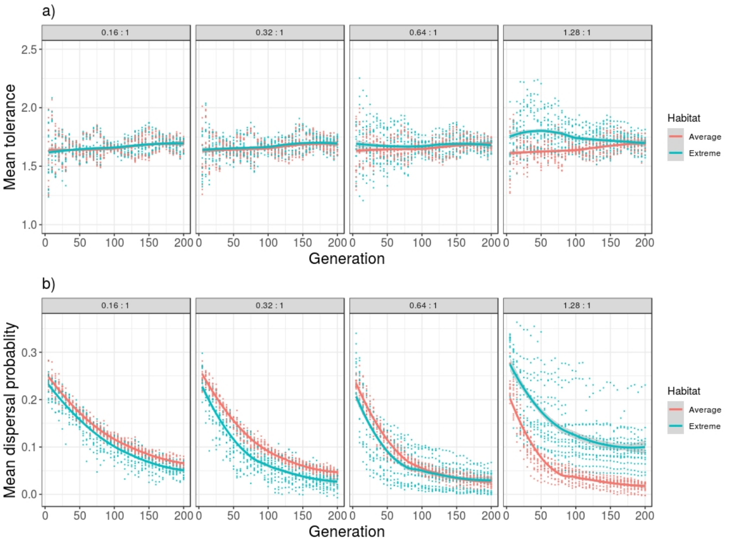

Figure S 6: a) Patch-wise mean tolerance values over time, starting in the fifth generation for two patches per landscape. For each of the 15 replicate simulation runs (5 landscapes x 3 time series) the patch with the most extreme habitat (the patch with the highest absolute value for the habitat attribute; blue dots and line) and the patch closest to average conditions (the patch with the lowest absolute value for the habitat attribute; red dots and line) are shown. b) Change in patch-wise mean dispersal probability trait values over time, starting in the fifth generation for average (blue dots and lines) and extreme habitats (red dots and lines). Arrangement and classification of panels as in Fig. 4

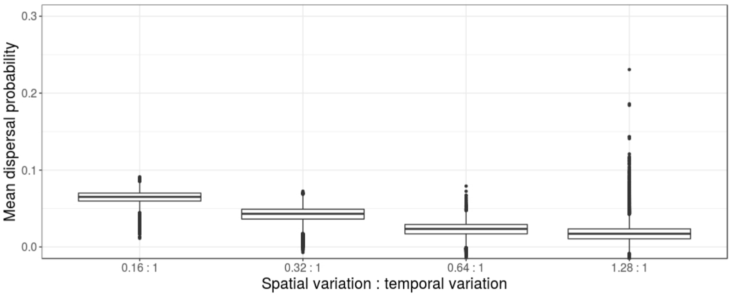

Figure S 7: Box-plot of mean evolved dispersal traits values (averaged over 15 replicate scenarios) for the different degrees of spatial variation. Spatial variation increases to the right and is labeled relative to the temporal variation of 1.

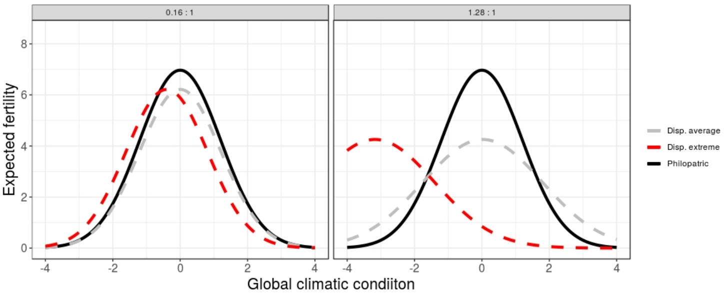

Figure S 8: Expected mean fertility for individuals either remaining philopatric and adapted to the patch of origin ($h_i = \bar{H}_j$) in dependence of actual climatic condition (black line) or randomly dispersing, accounting for 10% dispersal mortality. Grey hatched line for individuals adapted to and emigrating from an average patch ($H_j = 0$) and red hatched line for individuals adapted to conditions -2.5 spatial standard deviations below the spatial mean (cold adapted). Top row shows values for the strong $\alpha = 2$, bottom row for the weak trade-off ($\alpha = 4$), left column shows values for the lowest spatial variation (sd = 0.16), the right column for the highest spatial variation (sd = 1.28).

7 Landscape structure and spatio-temporal heterogeneity influence emigration rate more than emigration strategy

Since the assumption of global random dispersal is often not justified, we wanted to further investigate different dispersal strategies. Additionally, we were interested in the actual influence of different landscape configurations and of ecotone structure on the evolution of the environmental niche and dispersal. Therefore we extended the simulations from the previous manuscript to a larger set of landscapes, both with gradual and abrupt ecotones and included short-distance emigration, either random or dependent on the individuals' fitness in their natal patch.

This manuscript is in preparation to be submitted to a peer-reviewed journal.

I implemented the simulation model, analysed the results and drafted and wrote the manuscript. Thomas Hovestadt contributed to the manuscript and the conceptual framework.

My overall contribution amounted to 95%.

7.1 Abstract

Dispersal is an important event for most organisms at least once in their life cycle. The evolution of dispersal can be influenced by local adaptation, landscape structure, and perceived temporal and spatial variation. Here, we implemented an individual-based model (IBM) of trait evolution in a metapopulation, with scenarios characterized by different landscape structure and different degrees of spatial heterogeneity and global temporal variation. Individuals could evolve in two traits coding for the environmental niche (position of niche optimum and niche width) and two traits determining nearest-neighbor dispersal: an individual emigrates with a probability defined by the first trait (random emigration) but emigrates with certainty if the expected fertility in the patch of residence falls below a fertility threshold specified by the second trait (habitat dependent emigration). We show, that even though there is a difference in emigration rates between emigration strategies (more emigration under habitat dependent emigration), the effect of landscapes structure is more dramatic. Landscapes with very distinct edges between habitat clusters result in a high degree of spatial sorting, while autocorrelated landscapes do not. Emigration rates are overall lowest, when spatial variation is highest, even as low as zero in certain landscape types. We therefore conclude, that emigration rate is influenced more by landscape structure and spatio-temporal heterogeneity than by the emigration stategy. With the ongoing land use change more research into this could also help shed light on the difficulties species might be facing under the change from landscapes characterized by gradual ecotones to landscapes with abrupt ecotones, the latter typical for agricultural and urban settings.

7.2 Introduction

Dispersal is an important behavior of most organisms at least once in their life cycle. Dispersal can facilitate survival, lead to avoidance of kin-competition and of poor habitat conditions (Barnes et al. 2015; Bowler and Benton 2005; Clobert et al. 2009; Cobben, Verboom, et al. 2012; Goff et al. 2019; Mortier et al. 2018; Romero-Mujalli et al. 2018). In a previous study, we could show that the relationship between spatial and temporal variation in environmental conditions may influence the evolution of emigration probability but not of local adaptation under random global dispersal (Sieger and Hovestadt, 2020 in review). Other types of dispersal with more limited dispersal distance, however, were not investigated, even though they were shown to be highly important in nature, and to both, influence the evolution of local adaptation (Bowler and Benton 2005; Bridle et al. 2019; Jacob, Laurent, Haegeman, et al. 2018; Kisdi et al. 2020) and itself being influenced by local adaptation (Kisdi et al. 2020).
The simplifying assumption of global dispersal is wide-spread in modelling approaches, but disregards the tripartite composition of the dispersal process. Individuals or propagules have to leave their natal habitat patch (emigration), move between habitats, and immigrate into the new patch (Bowler and Benton 2005; Crook et al. 2017). Emigration can be population dependent (e.g. density dependent) or state-dependent (e.g. fitness or life stage dependent) (Bona et al. 2019; Cronin et al. 2020). Habitat choice is an important immigration strategy and was shown to evolve faster than local adaptation (Kisdi et al. 2020), but in turn accelerates local adaptation (Camacho et al. 2020; Jacob, Laurent, Haegeman, et al. 2018). This is contrary to the classical view of dispersal as an antagonist force undermining local adaptation; in particular during range shift, dispersal can lead to colonization by maladapted individuals at the range front (Cobben, Verboom, et al. 2012). The same can be said for patches which are less connected with the core habitat and that depend on immigration for continuous occupation (sink patches). Here the asymmetric gene flow from source patches (core habitat) can lead to local maladaptation (Kawecki 2008). Weiss-Lehmann and Shaw (2020) could show that in sexually reproducing species, increased dispersal can lead to gene swamping via increased gene flow and therefore reduce local adaptation. Overall, dispersal can thus have two effects on local adaptation: 1) reduction of mean fitness caused by the immigration of maladapted individuals which changes mean trait values and / or trait variation, 2) or increase of fitness either by increasing the genetic variation,

which increases evolutionary potential (Bridle et al. 2019) or by enhancing local adaptation via immigration of individuals that choose habitat matching their niche attributes (Jacob, Laurent, Haegeman, et al. 2018; Kisdi et al. 2020. However, which of those effects emerges in a population also depends on the the spatial structure of the landscape the metapopulation inhabits (Bridle et al. 2019; Jacob, Chaine, et al. 2019).

The most apparent way how landscape structure can impede dispersal, is landscape fragmentation (Barnes et al. 2015; Jacob, Laurent, Morel-Journel, et al. 2020). If suitable habitat is (too) far apart to easily disperse, selection for dispersal can weaken (Kubisch, Degen, et al. 2013; Sinai et al. 2019). Even in non-fragmented landscapes, landscape heterogeneity can influence the evolution of dispersal, since an organisms dispersal ability determines the environmental variation it encounters during its lifetime. (Bridle et al. 2019; Kaemingk et al. 2019; Schiffers et al. 2014). If an individuals disperses far (searches widely) and frequently in heterogeneous landscapes, they will encounter a wider variety of environmental conditions. Landscape heterogeneity is usually considered to be detrimental to the evolution of frequent dispersal (Bridle et al. 2019; Kaemingk et al. 2019; Kubisch, Degen, et al. 2013; Schiffers et al. 2014; Sinai et al. 2019). In principle, landscape heterogeneity could also be beneficial, since it increases the chance to encounter new habitat where the conditions fit the individual's niche optimum better. Without informed or habitat-orientated dispersal though, increased dispersal also increases the probability of encountering adverse conditions in the new habitat (Clobert et al. 2009; Kubisch, Holt, et al. 2014). Increased dispersal can still be feasible though, for generalist individuals that do not experience a (pronounced) fitness-decline in a wider array of habitat conditions. Without habitat-oriented dispersal or generalist dispersers, only landscape homogeneity will lead to increased dispersal probabilities, since dispersal is no longer penalised by an increased possibility to encounter unsuitable habitat. In this case population density could be similar across the whole landscape and therefore decrease the expected differences in fitness expectation. This would eventually leave avoidance of kin-competition as the primary benefit of dispersal (Poethke, Pfenning, et al. 2007). Additionally, dispersal can also be used to compensate momentary adverse conditions in temporally variable landscape. Here, dispersal can help find a habitat that is, in this particular period (e.g. year, season) more similar to the optimal conditions of an individual, even though it might not show optimal conditions in average time periods. Temporal variation in the habitat conditions could shift the overall average conditions in the "right" direction, so that individuals that would not have high fitness expectations in average years, have higher fitness expectations in more extreme years. We could show, that especially in patches that deviate far from the landscape mean, individuals evolve high dispersal probability, when spatial variation is high. This bet-hedging strategy leads to higher fitness expectations of dispersers than philopatrics in extreme years (S. and Hovestadt n.d.). This could further be advanced by selectively emigrating, when fitness expectations are low.

Additionally, Schiffers (2014) showed in a simulation study that not only the heterogeneity at large but also the geometry of a landscape can influence the evolution of dispersal. In checkerboard landscapes, with distinct edges between patches, the grain size (i.e. the size of a cluster of patches with the same attribute) highly influenced the speed of range expansion, as well as other population characteristics. In gradient landscapes the evolved dispersal distance depended on the length of the gradient: shorter gradients favoured shorter dispersal distances, while longer gradients selected for longer distances. Furthermore edge effects (Kaemingk et al. 2019), as well as patch connectivity (Fobert et al. 2019; Masier and Bonte 2020; Schwarzmueller et al. 2019; T. Cronin et al. 2020) and structure of the natal habitat (Ducros et al. 2020) have been found to shape dispersal syndromes. Overall, this leaves the impression that landscape structure can strongly influence dispersal.

Furthermore, we could previously show that the relationship between spatial and temporal variability influences the shape of the trait space and can lead to the development of bet-hedging strategies (Sieger and Hovestadt 2020, in press) with dispersal as a strategy to compensate for global temporal variance in habitat conditions. This effect of the degree of spatio-temporal variability can be especially important if temporal variability in habitat conditions has a different scale than spatial variability.

7.2.1 Research goals and hypotheses

The insight and findings mentioned above suggest that the interaction between local adaptation, landscape heterogeneity, temporal variability and rules of dispersal may be more complex than previously assumed. Here we want to examine such interactions between landscape structure and in especially investigate the role of emigration rules on emerging dispersal rates and local adaptation. In particular we hypothesise the following: Hypotheses: I) Bigger habitat clusters or larger Hurst index in case of autocorrelated landscapes lead to more emigration (into similar habitat). II) In landscapes with sharp transition zones (edges), there will be lower emigration rates at habitat cluster edge and therefore spatial sorting of phenotypes. III) Habitat dependent emigration results in higher overall emigration than random emigration. We expect the disadvantages of emigration to be alleviated when emigration only happens, when fitness is low, since the fitness expectations in a new patch are more likely to be better than the expected fitness in the natal patch, when the latter is already rather low. IV) Emigration decreases with increasing spatial variation, regardless of emigration strategy.

7.3 Material and Methods

For this study, we expanded the metapopulation model of annual, haploid individuals already described in Sieger & Hovestadt (in press) to a set of simulations in differently structured landscapes and implemented different dispersal strategies, using the programming language julia (Bezanson et al. 2012). Each patch of a landscape (grid-cell) is characterized by a certain habitat value so that the landscape exhibits spatial variability in habitat features. These values can be interpreted as reflecting habitat related variance in global conditions like temperature or precipitation, but every other environmental variable varying over a continuous space is just as likely (e.g. soil nitrogen content, water oxygen content, pH, or salinity). As explained in more detail below, habitat attributes also underlie global temporal variability so that conditions in any patch are variable in time but such variability is completely synchronized across the landscape. Each habitat patch in the metapopulation houses one population as described in Sieger et al. (2019). Individuals can disperse to other patches determined by either one or two traits. We use fertility (expected number of offspring) as a proxy for fitness. For each individual, fertility depends on the fit between an individual's niche optimum and current environment condition as well as the individual's niche width (see below). The dispersal traits and both niche traits mutate during inheritance thus allowing for adaptation to simulated conditions. This will be explained in detail below.

7.3.1 Landscapes and scenarios

The metapopulation covers a spatially heterogenous landscape of 64 by 64 habitat patches wrapped into a torus. They are either clustered landscapes characterized by sharp edges or more gradual, autocorrelated, periodic (fractal) landscapes. The first were created with the NLMR-Package (Sciaini et al. 2018) in R (Team 2018) using the nlm_randomrectangular_-cluster() tool. The second were created with an algorithm for autocorrelated (fractal) landscapes with a given Hurst-Index, developed by Chipperfield et al. (2011). We standardized each resulting landscapes to the mean value of 0, by calculating the mean of the landscape and subtracting this mean from each patch's value. For avoiding unaccounted variance between simulation experiments we created and stored ten different realizations of both types of landscapes, autocorrelated and clustered, grouped into two groups. Each group is for one of the two patch cluster sizes (small and big) we examined. This lead to four distinct landscape scenarios: autocorrelated landscapes with big habitat clusters, autocorrelated with small habitat clusters, clustered landscapes with big habitat clusters and clustered landscapes with small habitat clusters. Neighboring patches with a similar environmental value are considered a habitat cluster. This distinction is more clear in the "clustered" landscape type, since the edges between habitat clusters are clear cut. At the edge of a habitat cluster, the neighboring patches on the outside of the habitat cluster have different values than the patches in the cluster whereas all cells in one habitat cluster have exactly the same habitat value. In the fractal landscapes however, the environmental values of neighboring patches follow a gradient without clearly defined edges. These landscapes are best described by their degree of autocorrelation, i.e. the Hurst-index.

The landscapes used as fractal landscapes with small patch cluster sizes (Hurst-index of 0.3) were the same as the ones used in Sieger & Hovestadt (in press). To achieve similarly variable landscapes for the other three landscape styles, we created more landscapes then needed with the above mentioned algorithms (fractal with a Hurst-index of 0.9 and clustered with bigger or smaller patch clusters) and chose five that matched the variance and standard deviation of the five landscapes used in Sieger & Hovestadt (in press). With this, we achieved two groups of each landscapes type, with small or big habitat cluster sizes that had sufficiently similar standard deviations to match the first set of landscapes, leading to four landscape styles (see 7.2 a)).

Each landscape additionally experiences global temporal environmental variation: at the beginning of every time step t a random value, drawn from a normal distribution with mean=0 and $\sigma_T = 1$, is added to any patch's mean environmental value to form the current environmental value of each patch – as a consequence local conditions vary in time thus modulating an individuals' fitness expectations. For repeatability and to avoid unaccounted variance we created three different time series of environmental variation, that are utilized in all of the simulation experiments described below. All following landscape scenarios will thus be based on 5x3 replicated simulation runs per landscape style.

7.3.2 Life-cycle and population dynamics

Newborn adult individuals first "decide" whether to disperse. Each individual has a heritable and mutable trait d that codes for the probability to leave its natal patch. In some scenarios, only this trait defines the individual's random emigration probability $p = d$. However, in other scenarios a second dispersal trait f encodes an emigration fertility threshold: if the expected fitness falls below f the individual certainly emigrates with $p = 1$. Otherwise it emigrates with it's base probability $p = d$. An individual leaves the natal habitat, when a random number drawn from a uniform distribution $U[0..1]$ is lower than the individual's dispersal probability p. An emigrating individual either dies with a given dispersal mortality ($m = 0.1$) or immigrates into a patch randomly selected from the the eight neighboring patches. Individuals therefore either exhibit a random nearest neighbor dispersal (referred to as NN) or random nearest neighbor dispersal with habitat (fitness) dependent emigration (referred to as HE). We did not include habitat choice or scouting into our dispersal strategies.
After dispersal, density-independent but habitat dependent reproduction of the N_j adults i in each patch j takes place. The fit between environmental conditions and the individual i's niche, determines its reproductive success: the individual's expected fertility is defined by two heritable traits, the position of the niche optimum h_i in the environmental space and the niche width (tolerance) g_i. Combined, the two traits define a normal distribution for the expected fertility around the niche optimum. The expected number of offspring for each adult i is thus calculated, with inclusion of a generalist-specialist trade-off term (equation (7.1)), following Chaianunporn et al. 2015). The resulting, environment dependent expected number of offspring for adult i with traits h_i and g_i in patch j, $L(H_{j,t}, g_i)$ at time t is calculated as:

$$L(H_{j,t}, h_i, g_i) = R_0 \cdot T_i \cdot e^{\frac{-(H_{j,t}-h_i)^2}{g_i^2}} \tag{7.1}$$

with R_0 the maximum possible offspring number. The trade–off is calculated as:

$$T_i = e^{\frac{-g_i^2}{2\alpha^2}} \tag{7.2}$$

Note that larger values of α imply lower trade-off costs.

When the difference between h_i and $H_{j,t}$ is low or the value of g_i is high, $L(H_{j,t}, g_i)$ is also high. The actual number of offspring (larvae) born by each adult i in patch j is then generated by drawing from a Poisson-distribution with mean $L(H_{j,t}, h_i, g_i)$. The offspring inherit the four trait values from their parent, changed by a mutation event (see below). After the birth of all offspring, the adult population dies.

Finally, the total number of larvae $L(j,t)$ produced in patch j at time t undergo density-dependent mortality, with survival probability calculated according to the Beverton-Holt-model:

$$s_{i,j,t} = \frac{1}{1 + a \cdot L(H_{j,t}, g_i)} \tag{7.3}$$

with $a = \frac{R_0 - 1}{K \cdot R_0}$ and K the carrying capacity. This survival probability is used to allocate a random binomial factor to each individual offspring indicating whether it survives or not; the surviving larvae constitute the new adult population of the next generation. One time step t therefore equals one generation.

All four trait values of an individual are inherited from the parent and evolve by mutation and selection (see below). Evolution of the niche optimum and dispersal traits are not penalized, but according to equation (7.1) enlarging niche width underlies a trade-off of different strength (parameter α). Since previous studies (S. and Hovestadt n.d.; Sieger et al. 2019 as well as preliminary simulation runs (data not shown here) did not detect a qualitative difference in trait evolution with a stronger trade-off, we only implemented a weak trade-off. The traits of each individual mutate separately and in each generation according to the following rules. A value drawn from a normal distribution with mean 0 and standard deviation 0.03 is added to the niche optimum inherited from the parent. The tolerance trait value that must be restricted to a range >0 is multiplied with a value drawn from a uniform distribution between 0.97 and 1.03. The dispersal probability d and the fertility threshold f are also changed additively by adding a value drawn from a normal distribution with mean 0 and standard deviation 0.001. Values for d can thus also take values outside the range [0 ..1] but this is not problematic, since the dispersal routine implemented treats dispersal with $d < 0$ as $d = 0$ and values of $d > 1$ as $d = 1$. Note that in the NN scenarios the fertility threshold becomes a neutral trait as it does not affect the dispersal behavior.

7.3.3 Initialization and scenarios

All 64x64 patches in a landscape were initialized with 100 individuals each. Each individual was initialized with a niche optimum drawn from a normal distribution with the environmental attribute of their natal patch as mean and a standard deviation 0.2. The niche width (tolerance) was drawn from a Log-normal distribution with σ_g and μ_g, which were calculated from the results for the last generation in the simulations of Sieger & Hovestadt (in press) for the same trade-off strength, to speed up the adaptive evolution. To calculate parameters μ_g and σ_g of the log-normal distribution from the evolved trait values g_i, the means m and variance v of g_i were inserted into the arithmetic moments of the log-normal distribution for mean (first moment, (7.4)) and variance (second moment, (7.5))

$$\mu_g = \ln\left(\frac{m}{\sqrt{1+\frac{v}{m^2}}}\right) \tag{7.4}$$

and

$$\sigma_g^2 = \ln\left(1+\frac{v}{m^2}\right) \tag{7.5}$$

The starting dispersal probability d for each individual is 0.2, while the fertility threshold f is drawn from a uniform distribution $[0..R_0]$, with $R_0 = 10$. The carrying capacity K of each patch is 1000 individuals.

To examine the influence of the relationship between temporal and spatial variation, we further created variants of the 20 landscapes with different spatial variation. In the original set of landscapes, the temporal variation had a standard deviation$\sigma_T = 1$ and the average spatial variation was $\sigma_S = 0.32$. To achieve the different relationships, we kept the temporal variation the same but multiplied each patch's habitat attribute with either 2, 4 or 8 ($\sigma_S \in 0.32, 0.64, 1.28, 2.56$). This lead to 80 distinct landscapes. Each landscape was used for modelling the metapopulation for three replicates, with the respective vector of temporal variation, each for the time span of 300 generations. This was done for both implemented dispersal strategies. Additionally, to explore the possible emergence of spatial structure in the fertility threshold f, nine additional replicate replicates of one identical landscape of each landscape type and habitat cluster size with habitat dependent emigration were performed; replication was done to enhance the visibility of (possibly weak) patterns in the spatial structure. Note that only replicates of the same landscape of each landscape scenario can be used, since the five different landscapes have differing spatial structures. For these nine additional replicates, we calculated the mean values of f of each patch over all replicates. This led to more visible spatial structures in the results, which were already found in the other scenarios.

7.3.4 Analysis

Graphical presentations of results were created using R (Team 2018) with the 'tidyverse' package (Wickham et al. 2019). No statistical significance tests on results were performed, since this is not meaningful in modeling approaches. For each patch in each landscape scenario the population means of all trait values, as well as the mean population size and fertility (as a proxy for fitness) were calculated and stored every fifth generation. Smoothed curves were fitted to the data using the "loess" method of the geom_smooth function, which uses a generalized additive model for fitting. Additionally, as a measure of neighborhood habitat heterogeneity, we selected every fifth patch in both dimensions and calculated the standard deviation in habitat attributes of the eight patches surrounding the target patch and the target patch itself. This measure is used to visualize the difference in the target patch's habitat attribute in relation to that of its neighboring patches. If the target patch is central in a habitat cluster, this neighborhood heterogeneity metric is low or zero and if the target patch is at the ecotone between two habitat clusters the metric is higher.

7.4 Results

In our simulations individuals adapted perfectly to the local conditions and even in extreme patches no adaptation gap can be found after 300 generations. This is the case regardless of landscape type, habitat cluster size or degree of spatial variation (supplementary information S1). The evolving niche width was also unaffected by the different scenarios and only depended on the trade-off strength (S2). The dispersal probability trait d as well as the fertility threshold trait f did develop a slight hump shape, when plotted over the patch mean value meaning that in more extreme habitats dispersal probability is lower than in average habitats; however, this effect was not very pronounced. The emigration probability trait d was however,

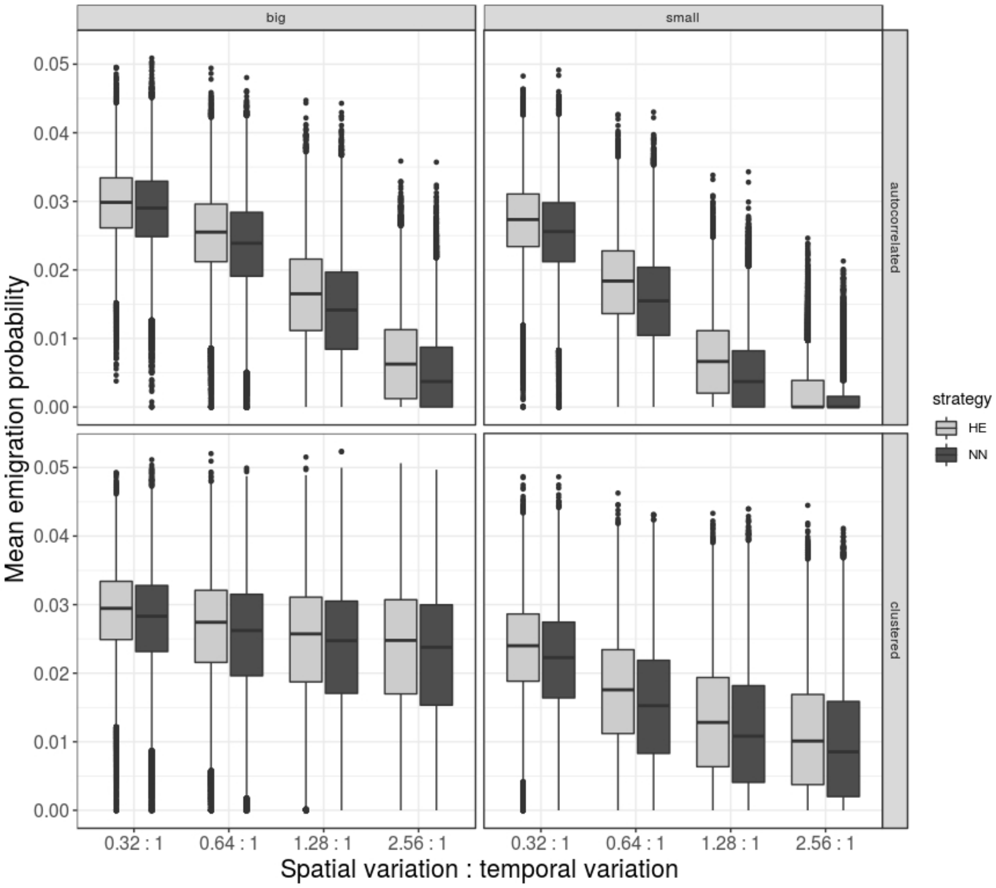

Figure 7.1: Mean emigration probability trait value d of each patch in the last generation. Dark grey indicates results for random nearest neighbor emigration (NN), while light grey indicates habitat dependent emigration (HE). The top row shows the result for the auto-correlated, the bottom for clustered landscapes. The left column corresponds to big habitat clusters, the right to small habitat clusters. In each panel, spatial variation increases from left to right, while global temporal variation stays the same ($\sigma_T = 1$).

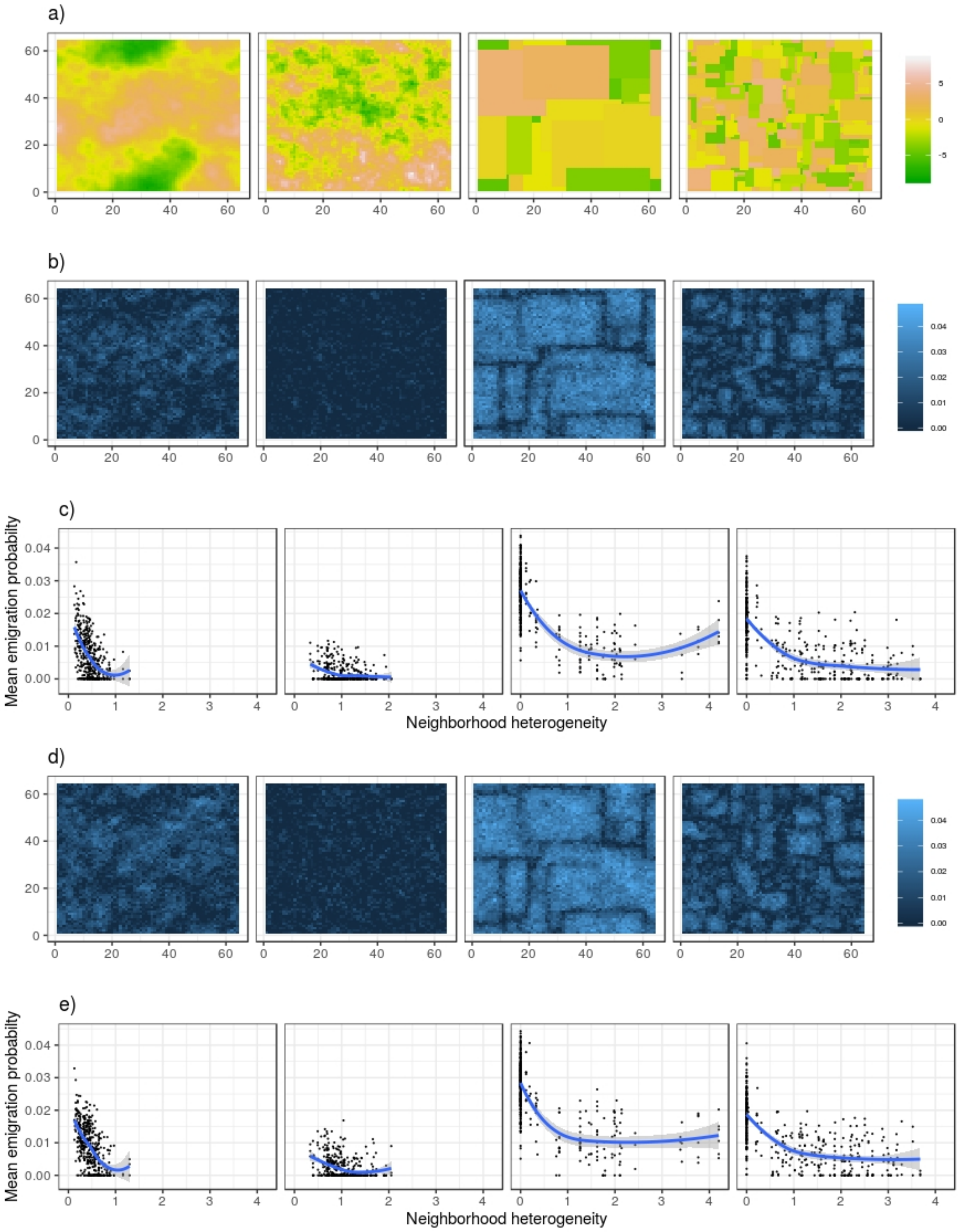
a)
b)
c)
d)
e)
0
20
40
60
5
0
-5
0.04
0.03
0.02
0.01
0.00
Mean emigration probability
Neighborhood heterogeneity
0
1
2
3
4

Figure 7.2

Figure 7.2 *(previous page)*: **a)** Exemplary landscape configuration for one landscape of each landscape type and each habitat cluster size. Auto-correlated landscapes with big (first panel; large H) and small habitat clusters (second panel; small H) and clustered landscapes with big (third panel) and small (fourth panel) habitat clusters. All following rows also show this configuration of panels. **b) and d)** Mean trait values of emigration probability d for each patch of the landscapes shown in row a) to illustrate the spatial sorting of d in clustered landscapes in scenarios with high spatial variation (2.56) and either random emigration (NN, b)) or habitat dependent emigration (HE, d). **c) and e)** Evolved patch mean trait value of d for all landscapes in the different landscape scenarios over the neighborhood heterogeneity metric for scenarios with high spatial variation and either random emigration (NN, c)) or habitat dependent emigration (HE, e). In clustered landscapes, the neighborhood heterogeneity reaches higher values than in auto-correlated landscapes but also has a higher proportion of very low values, due to the 'blocked' landscape configuration.

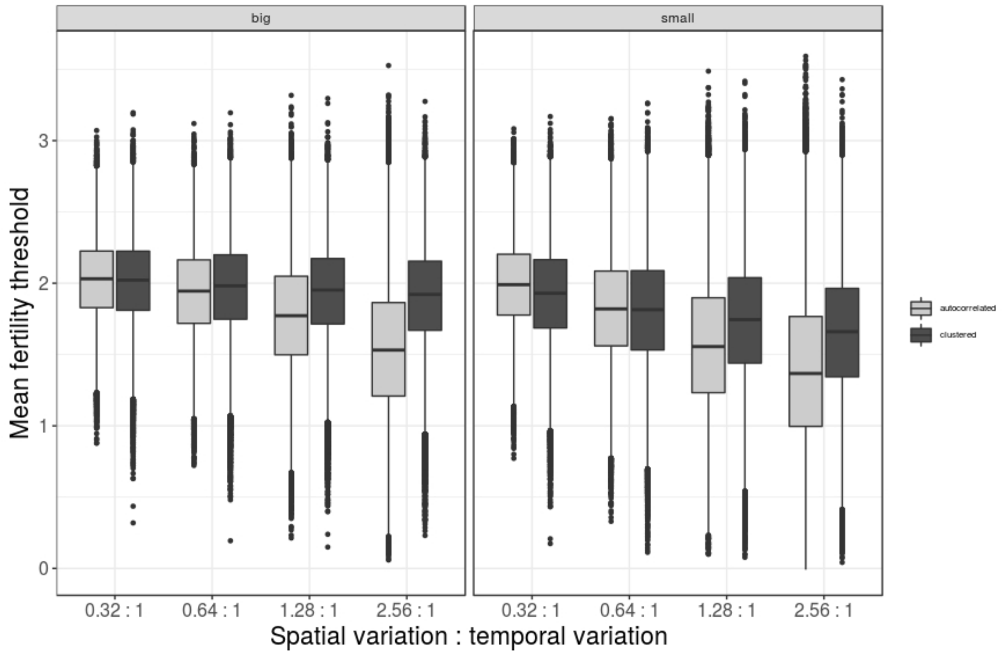

Figure 7.3: Evolved mean fertility threshold f in the last generation. Dark grey indicates results for clustered while light grey indicates results for autocorrelated landscapes. The left panel shows big habitat clusters, the right small habitat clusters. In each panel, the spatial variation increases from left to right, while the temporal variation stays the same ($\sigma_T = 1$).

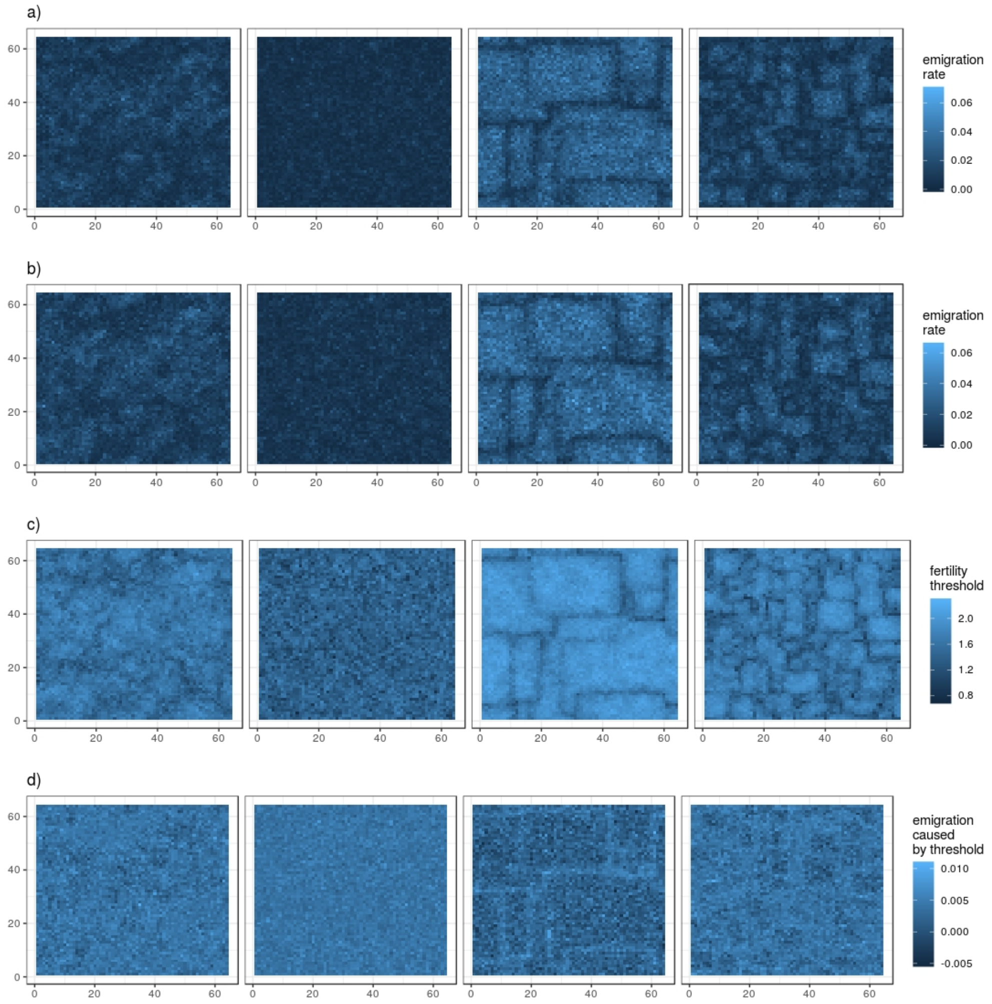
a)
b)
c)
d)
0
20
40
60
emigration rate
0.06
0.04
0.02
0.00
fertility threshold
2.0
1.6
1.2
0.8
emigration caused by threshold
0.010
0.005
0.000
-0.005

Figure 7.4

Figure 7.4 *(previous page)*: The results presented here are from the nine additional replicates of one landscape for each landscape type and habitat cluster size, following the same panel configuration and for the same landscapes as in figure 7.2. a) Spatial structure of emigration rates in scenarios with random emigration (NN). Evolved emigration rates shows edge effects (spatial sorting) in clustered landscapes (panel 3 and 4) b) Emigration rate spatial structure similar to row a), but for habitat dependent emigration (HE). Spatial sorting of emigration rate is the same as in row a). c) Mean fertility threshold f trait value, for scenarios with habitat dependent emigration (HE). In clustered landscapes spatial sorting of trait values of f (third and fourth panel) exists, while – particularly in the weakly autocorrelated landscapes, such spatial patterning is hardly recognized. d) Spatial structure of the difference between mean emigration rate and the emigration probability trait d of each patch in HE scenarios, to visualize in which patches emigration is caused by the fertility threshold trait f. When emigration is mainly caused by the baseline emigration probability trait d, the emigration rate is equal to the emigration probability trait, with some stochastic variation (caused by the stochasticity of the random baseline emigration). The value in this panel should then be approximately zero. If the emigration rate is higher than the emigration probability trait d, the surplus is based on emigration caused by the fertility threshold trait f. Again, spatial sorting can be found in the clustered landscapes, but not as pronounced as in the row above. In ecotones, emigration is more often caused by the fertility threshold trait f, i.e. by habitat dependent emigration.

highly influenced by the different landscape and spatio-temporal scenarios. With increasing spatial variation the trait value decreased. The magnitude of this decline, however, depends on both the landscape type, the habitat cluster type and the emigration strategy. In clustered landscapes the decline is less pronounced than in auto-correlated landscapes, resulting in evolution of higher emigration probabilities in clustered vs. autocorrelated landscapes if spatial variation is large. The lowest trait values are found in auto-correlated landscapes with small habitat clusters and high spatial variation, where almost all patches have a mean trait value of $dapprox0$. Except for scenarios with very low spatial variation (0.32), d is also higher in clustered landscapes and with habitat dependent emigration (7.1).

Particularly in clustered landscapes, the mean trait value of d in each patch also shows spatial sorting. The trait value is decidedly lower at the edges of habitat clusters and higher in habitat cluster centers whatever the degrees of spatial and whatever the emigration strategies (eg. spatial variation 2.56 in 7.2 b) and d)). With increasing neighborhood heterogeneity, the emigration probability decreases (7.2 c) and e)). This is especially pronounced in clustered landscapes with big habitat clusters and high spatial variation (7.2, b) and d), third panel in each row). In auto-correlated landscapes, less spatial structure in the trait values can be found (7.2, b) and d) first and second panel).

The trait coding for the fertility threshold f is a function-less (neutral) trait in the random emigration (NN) scenarios and consequently stays similar to the mean of the uniform distribution this trait was initialised from ($\bar{f} = 5$) if averaged over many replicates. In the scenarios with habitat dependent emigration, the trait value is selected towards mean values of around $\bar{f} \approx 2$ and lower. With increasing spatial variation, the fertility threshold decreases, with overall lower values in auto-correlated landscapes as compared to clustered landscapes. Small habitat cluster also lead to lower trait values of f, in both clustered and autocorrelated landscapes. Only when the spatial variation is very low (0.32) the difference between landscape type and habitat cluster sizes becomes negligible (7.3). However, the effects of landscape structure and spatial heterogeneity are generally less pronounced compared to the effct of the dispersal trait d. When examining the mean trait values of the nine additional replicates carried out for one landscape for each landscape type and habitat cluster size, a similar spatial sorting, as in the emigration probability trait d, can be found in the fertility threshold trait f. In clustered landscape, the spatial sorting is most pronounced in the landscape with big habitat clusters, while in autocorrelated landscapes, a pattern is hardly noticeable. At the edges of habitat clusters in clustered landscape, the trait values of f are distinctly lower than in the habitat cluster centers (**??** c)), suggesting lower emigration rates at the edges (7.4 b)). Consequently, the spatial sorting of both traits leads to generally lower emigration rates in the ecotones between patches. However, the spatial sorting of emigration induced by the fertility threshold trait f in clustered landscapes is nonetheless inverted: the difference between the overall emigration rate and the emigration probability trait d is highest in the edge patches, indicating that the surplus of emigration has to be caused by emigration due to low expected fertility; when emigration were mainly caused by the baseline emigration probability trait d, the observed emigration rate would equal the emigration probability trait (with some stochastic variation caused by the stochasticity of the random baseline emigration) (7.4 d)).

7.5 Discussion

The decreasing emigration rate with increasing spatial compared to temporal variation is rather evident and confirms our fourth hypothesis. With increasing spatial variation, the difference in habitat attributes between single patches and even more so between habitat clusters becomes more pronounced. Therefore, it is increasingly unlikely for individuals to be locally adapted to both, the natal and the (potential) new habitat. Consequently, emigration into another patch becomes increasingly penalized due to the decrease in fitness of immigrating maladapted individuals thus selecting for reduced dispersal (Hastings 1983; McPeek and Holt 1992). We find that (i) evolution of the tolerance trait g is dominated by the global temporal variance but (ii) hardly affected by the spatial heterogeneity (so that we do NOT see selection for larger values of g in more heterogeneous landscapes). Instead, just selection to avoid the risk by reducing the dispersal. The latter might be overturned if spatial variance becomes really small scale so that the local carrying capacity would be (really) small. In that case kin-competition would promote dispersal more strongly and thus might induce selection for larger g. The evolved individuals' tolerances are primarily a result of the temporal variability, leading to a higher impact of the temporal vs. the spatial heterogeneity, which we also found in previous studies (S. and Hovestadt n.d., in press). This was also found e.g. in Mediterranean salt marshes, where the high seasonality in high salt marshes influenced seed dispersal more than the spatial variation, opposed to lower marshes, where the spatial component is more influential than the seasonal (temporal) changes (Contreras-Cruzado et al. 2017).

Similar reasoning can lead to understanding the effect of landscape structure on the evolution of dispersal. In autocorrelated landscapes, neighboring patches likely have a different environmental mean, even if autocorrelation is strong. Indeed, almost no neighborhoods had zero deviation between patches in autocorrelated landscapes, whereas in clustered landscapes all patches of a habitat cluster share an identical environmental mean. This means that selection against dispersal is stronger in autocorrelated landscapes, since the dispersing individuals generally have a lower fertility than philopatric individuals. In clustered landscapes, at least in the centers of habitat clusters, there is no such penalty for leaving the natal patch, since an emigrating individual will receive the same fertility in the surrounding patches. This impact of higher inter-patch variation in autocorrelated landscapes is especially true in landscapes with high spatial heterogeneity and low autocorrelation and leads to the evolution of very low emigration in such landscapes. In strongly autocorrelated landscapes the inter-patch variation between neighboring patches is lower than in weakly autocorrelated landscapes. Equally, in clustered landscapes with small habitat clusters the probability of neighboring patch to be different from natal patch is larger as a larger proportion of patches will be located at cluster edges. This confirms our first hypothesis, that landscapes with large habitat clusters promote evolution of higher emigration rates. This was also found by several previous studies (e.g. 2010; 2012; 2006; 2014) Indeed, Vespa et al. (2018) found that edge effects on dispersal were less pronounced when the difference between native forest and monoculture plantations was lower. They could show that when plantations are new and therefore the difference between the plantations and the native forest was very high, seed dispersal into the plantations decreases. With ongoing plantation age, the contrast between the plantations and the forest diminishes, leading to increased seed dispersal from the forest into the plantations.

In addition to the inter-landscape differences of emigration rate, there is also the appearance of edge effects and spatial sorting, in particular when landscapes have a clustered habitat structure. Because of the aforementioned steep habitat gradient at cluster edges (ecotones), low emigration at habitat cluster edges is selected for; emigration across ecotones is severely penalized for locally adapted individuals by decreased fitness expectations in potential target patches. The relevance of this argument is also supported by the emergent disperal rates in some clustered landscapes (cf. Fig. 7.4), when neighboring habitat clusters have rather similar environmental mean. In this case, the edge effect is mitigated and more emigration between habitat clusters takes place. This confirms our second hypothesis. A comparable effect was indeed found in the ecotone between native forests and young plantations (Vespa et al. 2018). Similarly, the treeline ecotone also shows lower dispersal in both the boreal and the alpine treeline ecotone than the forest in lower altitude or latitude (Crofts and C. D. Brown 2020; Kambo and Danby 2018; Ribeiro et al. 2019. The dispersal across the boundary between forest and alpine meadows is encompasses a more drastic change in habitat conditions than dispersal inside the forest, where habitat conditions are more homogeneous. For specialized forest species dispersal from forest to wooded corridors is also lower (Paal et al. 2020), which is comparable to the situation in our simulations, since all individuals are locally adapted and can therefore be considered specialists of their native patch. Nevertheless, in scenarios with habitat dependent emigration, the rare emigration events in the edge patches between habitat clusters of clustered landscapes are more often caused by habitat dependent emigration (7.4 d)). This is however, explained by the overall lower fitness in the ectones. Individuals have lower fitness in the ecotone patches and therefore the threshold trait is more often higher then the expected fitness, leading to emigration.

Additionally, this could also have implications for conservation and restoration efforts. With ongoing land use change, sharp edged habitats become more prevalent (Liira et al. 2008). This could mean, that the trait distribution inside the habitat clusters also changes, from no spatial sorting of traits, like in the autocorrelated landscapes, to the spatial sorting found in the clustered landscapes. This change in spatial distribution of traits in habitat clusters could further the isolation of remaining natural habitats, by decreasing dispersal probability at the edges of habitat clusters. This would be especially damaging for species that rely on several types of habitat to thrive, for example anurans. It was already shown, that they severely suffer from the impact of habitat fragmentation (Homola et al. 2019; Ribeiro et al. 2019). The same mechanisms, that inhibit dispersal across sharp ecotones could consequently hinder the movement of anurean between their larval and adult habitats.

The most apparent distinction between the two emigration strategies is the evolution over time. While the emigration rate is up to a quarter of the population in the early generations of the scenarios with habitat dependent emigration, it is only up to about 5 % in the scenarios with random emigration. This is conceivable when considering that in the early generations following initialization, a high proportion of individuals is not locally adapted yet. This leads to lower fitness, which in turn leads to higher emigration rates, since the individual must emigrate, if its fitness falls below its threshold. With continuing evolution, the fitness threshold itself evolves, while the niche optimum simultaneously merges with the patch's mean environmental value. In the last years, only individuals that experience very harsh years experience such a low fitness (expectations) so that they emigrate. Apart from that, similar base line dispersal probabilities evolve, since there is no special selection for emigration. However, if other stressors would arise or the spatial configuration of the landscape would change, the individuals with habitat dependent emigration would be quicker to leave unsuitable habitats due to their fitness-dependent emigration. The randomly dispersing individuals would have to adapt their dispersal rates first to enhance the emigration probability. In the scenarios here nevertheless, there is little influence of the different dispersal strategies on the realized emigration rates after evolution reached an equilibrium, even though habitat dependent emigration leads to slightly higher emigration rates than random emigration, thus confirming our third hypothesis.

In our simulations, we only implemented short distance dispersal, i.e. individuals could only reach the patches in direct vicinity of their natal patch; this implies the assumption that the dispersal capabilities of species are limited in relation to the scale of spatial heterogeneity (possibly also because of selection for limited dispersal distance!). Limited dispersal distance is prevalent in various ecosystems and across ecotones. e.g. in halophytes in salt marshes (Polo-Ávila et al. 2019), southern Atlantic forest trees (Vespa et al. 2018), boreal forest plants and trees (Paal et al. 2020; Trant et al. 2018) and anurans (Ribeiro et al. 2019). However, it was also observed, that rare long distance dispersal is important for spread and colonization of new habitat, e.g. in eastern larch (Trant et al. 2018) or salt marsh plants (Polo-Ávila et al. 2019). It was also consequential in the speciation of neotropical lizards (Sheu et al. 2020). It would be interesting to investigate the evolution of long-distance dispersal events in future studies. In particular, we could show in a previous, study (S. and Hovestadt n.d.), that long-distance (global) dispersal can lead to bet-hedging effects against the effects of temporal variance, when the spatial variation of a landscape is high. In the current simulations, there is little selection in favour of dispersal, because short distance dispersal only takes individuals to similar patches. Therefore, there is no advantage to leaving the natal habitat patch, especially since dispersal is penalized at habitat edges or where steep gradients in habitat attributes occur. In subsequent simulations, either dispersal with an evolving dispersal kernel or dispersal switching between short- and long-distance dispersal could be implemented. The latter would be highly interesting, since it might be beneficial to mostly disperse to the neighboring patches, but simultaneously having the opportunity to disperse globally if the expected fitness falls below a certain threshold (due to extreme temporal variation). Then searching for a very different habitat could be favorable, if the new habitat is more suitable for the individuals phenotype under the conditions of an extreme year. This could be coupled with a mechanism for matching habitat-choice, to enable individuals to assess their expected performance in potential future patches and choose the most suitable one (cf. Camacho et al. 2020).

The presented simulation scenarios could additionally be enhanced by including several other aspects that were not included previously. In our simulations, no sexual reproduction took place, possibly slowing down the emergence of optimal trait combinations due to the lacking recombination. It was shown shown that sexual reproduction can be an important aspect in withstanding climatic stress. Trant et al. (2018) could show that in black spruce sexual reproduction was more susceptible to climatic conditions than clonal reproduction. This could mean that the influence of spatial or temporal heterogeneity on the evolution of the environmental niche and dispersal changes, when sexual reproduction were to be included. The evolution of the environmental niche and dispersal could of course also be influenced by competition with or facilitation by other species, which was not accounted for in this study. We also did not include the other two phases of dispersal, immigration and establishment, which also have an important role in colonization of new habitat and were shown to directly hinder dispersal, e.g. at treeline ecotones (Crofts and C. D. Brown 2020; Kambo and Danby 2018; Paal et al. 2020). A combination of multi-species interaction and dispersal could also be of interest. Vespa et al. (2018) argue that the increased dispersal of forest tree species into plantation with increasing age of the plantation is most likely due to the return of bats and birds into the plantations and surrounding forest, which facilitate the dispersal of more diverse seeds. Nevertheless, the resulting lower emigration rate was also found here and since the emigration mechanisms is not explicitly included, all kinds of emigration mechanisms are implicitly accounted for.

Overall, we could show that the landscape structure is paramount in the evolution of dispersal, especially when considering the differing degrees of spatial variation compared to temporal variation. With the ongoing land use change more research into this topic could also help shedding light on the difficulties species might be facing under the change from landscapes characterized by gradual ecotones to landscapes with sharp edged ecotones, which particularly occur in agricultural and urban settings.

7.6 Acknowledgments

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Supplementary information to ”Landscape structure and spatio-temporal heterogeneity influence emigration rate more than emigration strategy”

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2020

1 Local adaptation in the niche optimum and niche width

In our simulations individuals adapted perfectly to the local conditions and even in extreme patches no adaptation gap can be found after 300 generations. This is the case regardless of landscape type, habitat cluster size or degree of spatial variation (S1). The evolving niche width was also unaffected by the different scenarios and only depended on the trade-off strength (S2).

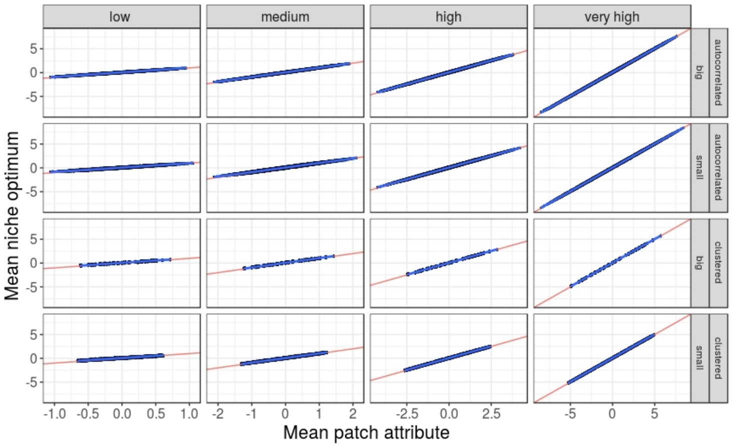

Figure S 1: Local adaptation in the niche optimum trait (blue line) for all degrees of spatial variation and all landscapes scenarios. In each row, spatial variation increases from left to right, while global temporal variation stays the same ($\sigma_T = 1$). Individuals are adapted perfectly to local conditions (red line).

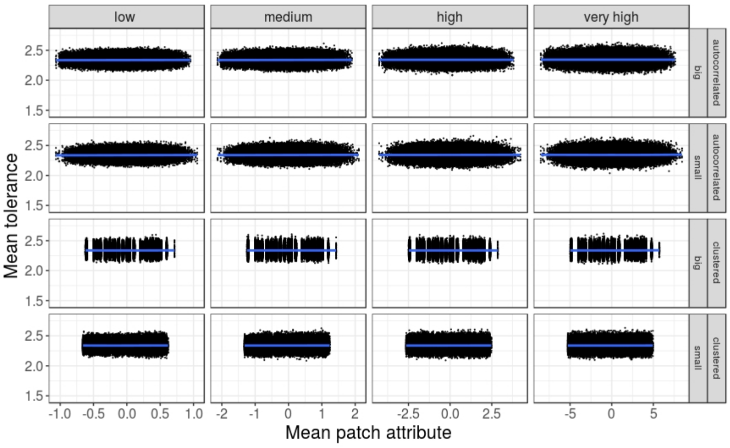

Figure S 2: Local adaptation in the tolerance (niche width) trait (blue line) for all degrees of spatial variation and all landscapes scenarios. In each row, spatial variation increases from left to right, while global temporal variation stays the same ($\sigma_T = 1$). Tolerance is not influenced by either landscape type, patch size or degree of spatial variation.

III | Discussion

8 | General discussion

8.1 Summary

In my work presented here, I wanted to disentangle the combined effects of spatial and temporal heterogeneity on the evolution of dispersal and individual niche traits. I therefore designed and implemented an individual based mechanistic model of a single population exposed to temporal variation of a habitat attribute and then extended this model to metapopulations. I could show that overall, spatial and temporal heterogeneity, neither of which have been included extensively in previous simulation work, have a big impact on the evolution of individuals. Just considering isolated populations I could show that increasing temporal variance can have a more problematic influence than increasing mean on population survival and can lead to conditions that must lead to extinction (see section 2.1). To include spatial variation on a landscape level, the previous model was then extended to the metapopulation level. Here I could show that, when the degree of temporal variation stays constant over time, but the spatial variation increases, the emerging trait spaces of the environmental niche and of dispersal traits differ with degree of spatial variation. Individuals‘ tolerance is not influenced by spatial heterogeneity but only by the implemented specialist-generalist trade-off and, more importantly, by temporal variance. Increasing spatial variance does not lead to increased tolerance. When spatial variation is lower than temporal variation, individuals emigrate most often from average habitats, while individuals from extreme habitats remain philopatric. With increasing spatial heterogeneity though, this relationship is reversed: There, individuals from average habitats rarely emigrate but individuals from extreme habitats disperse more often (assuming global dispersal). This can be considered a bet-hedging strategy in the extreme habitats of landscapes with a high degree of spatial variation (chapter 2.2.). Not only the degree of spatial to temporal variation is important: How spatial variation is structured in a landscape influences the emergent trait spaces more than e.g. the emigration strategy.

Employing the model on a set of different landscapes shows that landscape structure modulates edge effects and consequently the evolution of traits in different habitat patches. When landscapes include highly contrasting ecotones, as is the case e.g. in agricultural landscapes, individuals in edge habitats almost never emigrate. At the same time, emigration rate in the center of patches may be very high. In more natural, autocorrelated landscapes, no such expressed spatial sorting of traits was found (chapter 2.3.). Altogether, this highlights the importance of including the projected changes of temporal and spatial heterogeneity into predictive models of species survival and distribution, because they might affect our projections more than previously anticipated. Additionally, this could also have implications for nature protection, since sharp edges between natural and agricultural patches could hinder the re-colonization of other habitats, simply caused by edge effects.

8.2 Climate change and landscape structure

Throughout the work presented here, the influence of both climate (or any other change of a quantitative habitat attribute) change and landscape structure on the evolution of niche and dispersal became apparent. I first explored the evolution of the niche in isolated populations undergoing different degrees of climate change. There, I could show that, if individuals express at least some environmental tolerance, they can adapt to increasing habitat means indefinitely provided that the change does not proceed too fast. This is due to the fact, that during the environmental change, the mutation that needs to occure to track the increase in mean, is rarely achieved in one step. Therefore, immediate adaptation to the new environmental mean is not possible and a certain degree of tolerance is necessary for individuals to survive, especially given the temporal variance of mean conditions. In nature, this would of course show a different pattern, since no organisms can track an increasing environmental mean forever e.g. if mean temperature were to keep rising as it did over the last 50 years, organisms were at some moment limited at the very last by the denaturing temperature of proteins. However, it does not seem likely that the mean global temperature will keep increasing as it is recently. Therefore, a realistic time span of increasing mean conditions might be manageable for organisms, given they have a certain tolerance, which is anyway needed for individuals to thrive in a temporally varying environment. If the increase in mean conditions is so fast that it reaches the outer boundaries of the

niche width (exceeds the tolerance), before the species could adapt to the increase in mean, it will suffer from reduced fitness or even extinction.
In the case of an increasing temporal environmental variation, as was e.g. predicted for precipitation, adaptation may be much harder. The necessary widening of the niche (i.e. increasing tolerance) to match the increasing environmental variation, is related to a decrease in fitness, if a specialist-generalist trade-off exists. If the environmental variance were to become too large, the costs associated with coping with such variance might become so high that survival would not be possible anymore. This could for example be found in the non-random survival of Galapagos finches during drought years. In those drought years, the distribution of available seeds shifted and mostly large and hard seeds were available. The highest survival was therefore found in large birds with large beaks, because only they were able to utilize this food source (Boag and Grant 1981). To understand this, one has to first follow the assumption of a specialist-generalist trade-off. It is often assumed that such a trade-off must exist (Huey and Hertz 1984; King, Daphne J. Fairbairn, et al. 2012; King and Derek A. Roff 2010; Rutschmann et al. 2016; Stephens and Wiens 2008; Turner et al. 2015), since without it, it would be hard to explain the (functional) diversity of species on earth – without trade-offs individuals could adapt to cope with about any conditions and at the same time also perform about optimal under any condition. Consequently, a single species could take over all biomes and we would not find other species (at least all observable diversity would just be neutral). However, already from a physiological point of view, development of tolerance is associated with costs. If a species (or individual) were to tolerate a wider range of e.g. temperatures, it needs some kind of heat stress resistance and cold resistance at the same time. Such resistance is usually linked to certain protective proteins and linked to physiological costs (Huey and Hertz 1984; Luhring and DeLong 2017; Ørsted et al. 2018). At the same time, heat-resistant proteins cannot be cold-resistant as well. Other similar cases can probably be found for most environmental attributes. The existence of a specialist-generalist trade-off was also confirmed empirically, e.g. in Jurriaans S. and Hoogenboom M. O. 2019; Nguyen et al. 2019. Whenever such a trade-off exists, it is consequently impossible to widen the niche to the necessary extent, when the increase in variation keeps going indefinitely. This and other fundamental constraints further limit the evolution of a boundary-free tolerance. It is not possible for an individual to have cover all trait spaces, e.g. be big and small simultaneously, therefore it cannot tolerate environmental conditions

were one of them is advantageous while the other would be a disadvantage. Tolerance of an individual consequently has to be bounded. There will always be a point in evolution, were selection of a wider niche will not be feasible anymore (chapter 2.1). To explore how spatial variance influences

all traits, especially whether tolerance will be influenced by increasing spatial heterogeneity, I extended the model to a metapopulation level. By extending the individual based model of a single population, the influence of spatial heterogeneity and landscape structure became apparent. Tolerance is mainly needed to compensate the influence of temporal variance and only the implemented trade-off strength influences the emerging tolerance trait value and subsequently fitness heterogeneity in space. For given values of temporal variance and trade-off strength, the optimal niche width can therefore be calculated. Since we implemented a specialist-generalist trade-off, evolution of a broader niche trades off against maximum number of offspring under optimal conditions. This is e.g. given in thermal performance curves (Rutschmann et al. 2016). Individuals (or species) that fare well under a wide variety of mean temperatures (generalists) have a lower maximum number of offspring under optimal conditions. This could be the case e.g. because generalists invest more energy in thermal tolerance (e.g. heat-stress proteins or heat avoidance behavior) than specialists. This higher investment in one behavior therefore depletes more energy in generalists than in specialists. Subsequently, generalists have less energetic reserves to invest into quality or number of offspring.

The niche width is not much influenced by spatial heterogeneity, which is mostly balanced by dispersal. Here, the implemented dispersal strategy has a large influence. With global dispersal and random emigration, dispersal evolves differently in landscapes with a high spatial variance than in landscapes with a low spatial variance. In landscapes with low spatial variance, individuals from extreme habitats disperse less often than individuals from average habitats. This philopatry is explained by the probability distribution of those habitat types in combination with the temporal variance. Extreme habitats are rarer than average habitats. Therefore, when the spatial variation is smaller then the temporal variation, individuals from extreme habitats have a very low chance of encountering suitable habitat and dispersal is selected against, because it lowers fitness expectations. However, when spatial variation is larger than temporal variation, the possibility of average habitats to be closer to extreme habitats in extreme years becomes higher and therefore dispersal can be advantageous for individuals adapted to extreme habitats. Of course, global random dispersal can also lead them to immigrate into highly unsuitable habitats, which is why I consider this a bet-hedging strategy (chapter 6).

With nearest neighbor dispersal and both random emigration as well as habitat dependent emigration spatial sorting emerges for a subset of landscapes but the difference between extreme and average habitats disappears. If individuals can only immigrate into neighboring patches, their probability to reach a similar patch is rather high, depending on the landscape structure. In autocorrelated landscapes, the difference between neighboring patches is usually low, especially when the habitat cluster size is large (high Hurst-index) and the degree of spatial variation is low. Individuals that are locally adapted to one patch, therefore are unlikely to gain or loose much fitness when they disperse to their neighboring patches. Emigration is neither strongly penalized nor selected for here and the primary selective pressure would be the above mentioned kin-competition. In natural populations inbreeding avoidance is also important in the evolution of dispersal (Hamilton and May 1977; Leturque and Rousset 2002; Poethke, Hovestadt, et al. 2003; Poethke, Pfenning, et al. 2007; Ophélie Ronce et al. 2000). In clustered landscapes, where the border between habitat clusters is sharp, individuals emigrating from a patch in the center of the habitat patch, always immigrate into a patch with the exact same habitat attribute. However, in edge patches, they have a high probability of leaving their habitat cluster and immigrate into a patch with very different patch attributes. Therefore spatial sorting of emigration rates emerges in this subset of landscapes. Patches with a high neighborhood heterogeneity (i.e. at one or even several borders between habitat clusters) have low mean emigration rates. This happens irregardless of emigration strategy, i.e. if individuals' emigration or has a baseline random component and an additional trait coding for a fertility threshold under which the leave their natal patch. In autocorrelated landscapes, spatial sorting is much less pronounced as such strong ecotones hardly occur.

However, in edge habitats the fertility dependend emigration contributes relatively more to the overall emigration rate than in patches that are not edge habitat. Comparable patterns where found in empirical studies (Ducros et al. 2020; Jacob, Chaine, et al. 2019; Kaemingk et al. 2019; Masier and Bonte 2020; Mayer et al. 2019; Polo-Ávila et al. 2019; Vespa et al. 2018), where habitat (i.e. fitness-) dependent emigration occurred particularly at ecotones.

Additionally, the scale at which individuals perceive the landscape heterogeneity and the scale with which they can disperse as well as the carrying capacity population size sustained by one habitat patch can also influence the selection on certain traits. Especially small carrying capacities could increase the selection for dispersal, since kin-competition and inbreeding increase with decreasing carrying capacity. This could in turn lead to situations where selection for dispersal could also lead to the selection of a higher tolerance. Here, I only implemented populations with a large local carrying capacity, which could mask the above mentioned effects.

All of the above shows the importance of both temporal and spatial heterogeneity on the evolution of individuals' niches and dispersal traits. The influence of the spatial heterogeneity is not limited to just the overall distribution of habitat attributes and the degree of spatial variation - the particular spatial structure (arrangement of habitats) of a landscape can also have a big impact.

8.3 Increasing variance

Given all of the patterns found in this thesis, the significance of both temporal and spatial variance is undeniable. This is especially important given that an increase in environmental (climatic) variance is predicted to occur in the future: temperature will fluctuate more, both in and between years, summer precipitation will vary more inter-annually, marine ph will also increase in variation and overall extreme weather events will be more frequent (Alexeeff et al. 2018; Bailey and Pol 2016; Crhová et al. 2018; Dillon and Woods 2016; Easterling et al. 2000; Fischer and Schär 2008; IPCC 2014; Rummukainen 2012; Shama 2017; Sofaer et al. 2017; Ummenhofer and Meehl 2017; Vasseur et al. 2014; Vázquez et al. 2017; Wahl et al. 2016). Given the fast development of land use, it seems also likely that not only the genaral frequency of (natural) habitats will change but also the spatial variation With climate change, the switch of agricultural sites between active use and fallow land might also be performed more often, leading to increased spatial variation.

The predicted increase in variation will most likely be of high importance for the persistence of species. Several empirical studies have already shown the susceptibility of various taxa to increased variability. Bartheld et al. (2017) showed that the individual (short-term) fitness of tadpoles was more affected by an increase in variance of water temperature than an increase in mean water temperature. Contreras-Cruzado et al. (2017) found that high seasonal variation influenced halophyte distribution in salt marshes. Hare habitat choice is also highly influenced by weather fluctuations (Mayer et al. 2019). Spatially heterogeneous environments were also shown to lead to lower populations sizes (Jacob, Chaine, et al. 2019) and metapopulations that undergo strong demographic fluctuations develop higher dispersal rates (Masier and Bonte 2020), which in turn could influence their fitness, when dispersing in a heterogeneous landscape. The ecological effects and stress created by climatic changes may not necessarily be direct, e.g. heat stress, but may also come about by indirect effects where, for example, drought years affect the availability of critical resources (Griffen and Drake 2008). Additionally, increasing spatial variance and increasing temporal variance might also interact. If e.g. short-term weather variability increases, habitat choice for hares might become more difficult, because they might have to switch habitat more often to find sufficient forage (Mayer et al. 2019). If in addition the spatial variability of the landscape changes finding suitable patches for e.g. raising their young might become almost impossible, since suitable patches might be too close to unsuitable patches and therefore too small. The difference between neighboring habitat clusters might also become too big to support sustainable meta populations. Increasing spatial heterogeneity was shown to lead to loss of functional connectivity, which can have severe impacts on the survival of metapoulations (Masier and Bonte 2020; Ribeiro et al. 2019; Schwarzmueller et al. 2019).

8.4 Changing landscape structures

Not only the spatial variability could change in the future. Changes in landscape structure are one of the main effects associated with land use change. Loss of natural habitat and fragmentation are immense threats to both the survival of individuals as well as the preservation of biodiversity (Crook et al. 2017; Crowley et al. 2019; Liira et al. 2008; Potts et al. 2016). Complete loss of a habitat can rarely be endured by organisms. Therefore the possible adaptations to fragmentation or partial habitat loss are more interesting. Especially the increase of both urban and agricultural areas over the past and its predicted continuation threaten species. When urban or agricultural areas spread, natural habitats are often disrupted. Amphibians were shown to be especially sensitive to this fragmentation (Homola et al. 2019; Ribeiro et al. 2019). Like all organisms that depend on several habitat types for survival (e.g. aquatic breeding habitats and terrestrial adult habitats in amphibians), the movement between habitats

is a crucial part. With increasing contrast between habitat clusters, habitat connectivity is lost and reproductive success is lower. But not only in species that require several types of habitat the loss of connectivity can have a big impact. When species depend on a metapopulation structure to be viable, decreased connectivity jeopardizes the survival of sink populations and therefore also the long term survival of the whole metapopulation (Mapelli et al. 2020; Masier and Bonte 2020; Tarabon et al. 2019).
Not only the survival of populations but also the phenotype of organisms can change, when landscape structure changes (Ribeiro et al. 2019). Under habitat fragmentation, selection works against dispersal. However, the few individuals in a population that do disperse can have a more pronounced disperser phenotype, especially when the matrix they have to cross to new habitat increases in harshness (Jacob, Laurent, Morel-Journel, et al. 2020). When habitat is partially lost, like alpine meadow habitats, diminished by forest encroachment, it can affect males and females differently in their phenotype, while at the same time not threatening the metapopulation persistence (Goff et al. 2019; Matter et al. 2020).

In addition to overall fragmentation and loss of habitat, also the change at ecotones can impact individuals and populations. In particular with the increase of agricultural land use and urbanization, natural habitats with gradual habitat transitions are displaced more and more by steep edges (Crook et al. 2017; Liira et al. 2008). In landscapes with a higher edge density the influence of edge effects becomes more pronounced and can influence the distribution of species and biodiversity in the landscape. Forest specialist plants, for example, depend on sufficiently large forest patches and cannot thrive in habitat corridors and edge communities (Liira et al. 2008). The change of trait distribution in habitat clusters where low dispersal is selected for in edge patches might strongly affect conservation and restoration efforts. The isolation of natural habitats caused by habitat fragmentation becomes even stronger when low emigration rate at edges emerges in clustered landscapes, characterized by sharp transition zones.
However, even in agricultural settings, the ecotone between natural and agricultural habitat does not necessarily stay constant. In tropical plantations for example, the structure changes with plantation age (Vespa et al. 2018) and the – in the beginning sharp – edges ‚soften‘ over time. These softer edges between older plantations and the natural forest around the plantations indeed lead to increased dispersal into plantations compared to the sharp edges of young plantations. This supports the idea that changes in trait distribution are imminent for conservatory efforts.

8.5 Transition periods

All of the above changes in spatial and temporal heterogeneity are particularly important when considering the transition periods, where change is ongoing and systems are not in equilibrium. Even though ecosystems can always be considered as undergoing changes, the expected anthropogenic changes have a more directed influence and happen much faster than any natural transition. Even though I did not include both spatial heterogeneity and temporal trends in one simulation (see chapter 8.7) , both are important aspects of global change and will shape the transition periods in nature and I will venture some speculations into what the combined effects could be. This is especially important when considering the evolution of increased tolerance during adaptation to new conditions that we found in ongoing temporal changes. Here, short term selective pressures can favor evolutionary unstable phenotypes,as found in the scenarios with a very steep increase in the mean environmental attribute (chapter 5). Seeing that increased tolerance usually comes with a reduced fitness, the short term selection for higher tolerance can be detrimental to survival, in particular when it takes too long to reach a new equilibrium state or no new equilibrium state can be reached because of ongoing anthropogenic change. Here, the combination of several attributes changing over time can interact and aggravate the situation even further, e.g. increasing temporal mean conditions or temporal variation in combination with increasing edge density could be more detrimental then either of the two on its own. The increasing edge density could lead to increased isolation of the habitat cluster and therefore limit the possibility to emigrate to a more suitable habitat, while simultaneously lowering the fitness expectations (Crofts and C. D. Brown 2020; Kambo and Danby 2018; Vespa et al. 2018). Whenever individuals would not have the opportunity to reach other habitats, that are about similar (since even for tracking temporal trend they should only disperse to slightly different habitats), they have to cope with their natal patches changing attributes. With very low dispersal rates, the reaction to temporal trends could be more similar to the one in isolated populations (chapter 5). The emerging adaptation gap or increase in tolerance to track the increase in mean or variance would additionally lower the fitness expectations, but could promote dispersal. Additionally, ongoing changes in landscape structure could undermine the possibility of dispersal as a solution to the local environmental changes. Even when one reduction of expected fitness on its own would not lead to extinction, the risk of the

combined fitness drops could very well lead to extinction or severe population size decreases.
Nevertheless, dispersal could also be selected for more under temporal changes, in order to reach more suitable habitat or habitat that is only becoming suitable. This is indeed reported often as the range shift towards e.g. higher latitudes or altitudes (e.g. Cobben and Kubisch 2014; Cobben, Verboom, et al. 2012; Dytham 2009; Rodriguez et al. 2019; Trant et al. 2018

8.6 Possible dual dispersal strategy

Even though I only implemented either long or short distance dispersal, the different advantages and disadvantages of long and short distance dispersal and possible trade-offs between the two strategies need to be considered. Short distance dispersal to neighboring patches might be favorable to avoid inbreeding depression and kin-competition (Poethke, Pfenning, et al. 2007; Ophélie Ronce 2007; Ophélie Ronce et al. 2000). Even though long distance dispersal would be most fit to spread kin as far as possible, the risk of immigrating into unsuitable habitat becomes higher with long dispersal distances (Hovestadt et al. 2001), therefore short distance dispersal might be more suitable as a consolidating dispersal strategy. It might however not be the best strategy, when searching for a new, suitable habitat, e.g. to escape deteriorating conditions in the natal patch. When the neighboring patches, which are reachable by short distance dispersal have the same environmental attributes, immigrating into them does not help alleviate environmental stress caused by large-scale, that is spatially synchronized temporal changes in patch conditions. Here, long distance dispersal might be the better strategy because, when dispersing into a far away patch, chances are that this patch does not experience the same degree of change or in fact provides, in an exceptional year, just the right habitat attributes. However, long distance dispersal can come with increased costs of dispersal, both the costs of phenotypic changes as well as the increased mortality risk of the long duration of being in non-suitable habitat in between patches and, without the ability to select the new patch, the risk of ending up in unsuitable habitat (Bonte et al. 2012; Crooks et al. 2017; Jacob, Laurent, Morel-Journel, et al. 2020; Ribeiro et al. 2019).However, when individuals can choose the new habitat, the dangers of long distance dispersal are ameliorated (Clobert et al. 2009; Crowley et al. 2019; Jacob, Laurent, Haegeman, et al. 2018).

Therefore, it might be beneficial to have the ability to combine both dispersal strategies, which is already found in nature (Trant et al. 2018). Nevertheless, the decision when to perform which type of dispersal is still crucial. When conditions in the natal patch and its neighborhood are not changing, and individuals are locally adapted to this patch, leaving it is most likely only beneficial to avoid kin-competition, inbreeding (Poethke, Pfenning, et al. 2007; Ophélie Ronce 2007; Ophélie Ronce et al. 2000) and of course when the population density becomes too high (Bona et al. 2019; T. Cronin et al. 2020) to be sustainable. Here the random short distance dispersal I implemented would be a good strategy. However, under extreme conditions (in extreme years), reaching new, suitable habitat becomes more important. In this case, habitat dependent emigration (i.e. emigrating when fitness is low) might be the strategy of choice, but coupled with long distance dispersal.
In addition to habitat choice, the bet-hedging effect of dispersal I found for environmentally extreme and rare habitats could be employed to spread the risk of long distance dispersal. If this were coupled with habitat dependent emigration, were individuals would only disperse, when their fitness is below a certain threshold, it could highly increase population sustainability. If emigration is dependent on the expected fitness (and therefore the habitat condition), it might be more beneficial, to do long-distance dispersal, because of the chance to actually encounter a different habitat. Then, the bet-hedging strategy evolved in random long-distance dispersal in extreme habitats might become more prevalent, also in average habitats. Nevertheless, the latter would still have a lower chance of finding suitable habitats, because in extreme years they will be generally rare.

Considering all of the above, we could expect either the evolution/emergence of two alternative strategies of long distance dispersal, coupled with generalism and short distance dispersal, coupled with specialism, or the evolutionof a dual strategy. The former might be more likely when organisms lack the ability to choose the new habitat, either because they can't assess habitat conditions or lack the ability for active dispersal. However, when organisms can actively choose their new habitat, the dual strategy might be the most beneficial strategy. There, short distance random dispersal could be the main strategy, e.g. to avoid kin competition and inbreeding and to reduce the risks encountered during dispersal while maintaining high fitness expectations in the natal and neighboring patches. If the habitat conditions were to drop (either temporarily due to climatic variation or permanently due to ongoing global change) and expected fitness were to decrease, organisms could perform long distance dispersal in combination with habitat choice.

8.7 Limitations and perspectives

Of course, simulation models emanate from a series of simplifying assumptions. Here I want to present some of the limitations of the assumptions I made in my models and the lack of certain mechanisms and consequently discuss how they could influence the outcome of future models.

The number and fitness of offspring can also be influenced by maternal or epigenetic effects and sexual recombination, which were not included in the model. Trant et al. (2018) could show that in black spruce sexual reproduction was more susceptible to climatic conditions than clonal reproduction. This could mean that the influence of spatial or temporal heterogeneity on the evolution of the environmental niche and dispersal changes, when sexual reproduction were to be included. Additionally, sexual recombination can also play an important role in the evolution of dispersal (Leidinger and Cabral 2020; Weiss-Lehman and Shaw 2020) allowing for faster evolution and recombination. In our simulations, genetic and phenotypic variability depend only on the variability of the population at initialization and the mutation events. However, for the analysis of the evolution of certain traits without interference of parental effects, asexual systems were deemed perfect by Drake and Griffen (2008). Nevertheless, the high standing variation in the founding population here ensured that inter-individual variability was high and sufficient phenotypic variability was present in the meta-population (Vincenzi 2014). Therefore, evolution is not limited by lack of genetic variance.

Nevertheless, Proulx and Teotónio (2017) have shown that in environments were the parental environment is not informative about the offspring environment, randomizing maternal effects can increase fitness. Here, tolerance is an individual trait that offspring inherit from their parent, with a certain degree of change. However, it would also be possible, that offspring tolerance changes with offspring niche optimum, leading to a risk-spreading strategy of the parent. A bet-hedging strategy was found in fish, exposed to unpredictable environmental variability (Shama 2015, 2017).

The evolution of the environmental niche and dispersal could of course also be influenced by competition with or facilitation by other species. Here we only incorporate competition of functionally similar lineages. Griffen and Drake (2008) noted that species interactions should be included when assessing extinction risks, since community ecology can alter the effects of environmental factors. Species competing for resources, for example, could worsen the effects of environmental change and lead to extinctions or different selection on traits and habitat preferences. For example Jacob et al (2018) could show that generalists prefer suboptimal habitats in the presence of specialists.

We also did not explicitly include the other two phases of dispersal, immigration and establishment, which also have an important role in colonization of new habitat and were shown to directly hinder dispersal, e.g. at treeline ecotones (Crofts and C. D. Brown 2020; Kambo and Danby 2018; Paal et al. 2020). Here, immigration is a random mechanism. A combination of multi-species interaction and dispersal could also be of interest. Vespa et al. (2018) argue that the increased dispersal of forest tree species into plantation with increasing age of the plantation is most likely due to the return of bats and birds into the plantations and surrounding forest, which facilitate the dispersal of more diverse seeds. Nevertheless, the resulting lower emigration rate was also found in my third study here and since the emigration mechanisms is not explicitly included, all kinds of emigration mechanisms are implicitly accounted for.

9 | Outlook

Of course, research is never truly finished and always opens new questions and spawns new ideas. Therefore I would like to present some of the possibilities to enhance and broaden the scope of the individual based models (IBMs) presented here.

The first and most obvious next step would be to combine the models of climatic trends in isolated populations with the models of spatial heterogeneity in metapopulations to see how they interact. As stated above, global change does usually not influence one without the other and science is expecting an increase in mean temperature and climatic variability all over the globe. Additionally, the growing human population makes agricultural and urban areas more prevalent. Consequently, the interaction between climate change and land use change are important and would be interesting to explore in an IBM.

In light of the presented possible dual dispersal strategy, it would also be compelling, to actually implement the possibility to switch between long distance and short distance dispersal, especially in combination with the evolution of both the baseline dispersal probability and the fertility threshold below which emigration takes places. Here, it would be of interest, whether certain trait syndromes evolve and in which combination specialism, local adaptation and dispersal strategy evolve. This could very well be done by adding a fifth trait to the phenotype, coding for the probability to perform long distance dispersal. Then, selection could act on this and form trait combinations of e.g. habitat dependent dispersers with long distance dispersal.

Here, it would also be highly attractive, to include the other stages of dispersal and not only implement habitat dependent emigration but also enable individuals to choose their new habitat, depending on e.g. expected fitness. The trait coding for the fertility threshold could be used to also evaluate the expected fitness in prospective new patches. If the expected fitness in the prospective patch is below a critical threshold, individuals could sample other available patches , either until a certain number of samplings has taken place or until a patch better than the natal patch is found. The former could also be used to implement the costs associated with dispersal. Since longer search times for a new habitat can increase the dispersal risk, the number of samples taken could also increase the dispersal mortality. Then it would also be possible to code the number of samples an individual takes (i.e. individuals' choosiness) as an evolvable trait to explore the distribution of choosiness in a population and the trait combinations emerging as possible trait syndromes.

Considering that in my simulations the current environmental condition of the parent environment does not provide much information for the offspring's future environmental condition, the influence of both the parental environment and the parental investment could be included in future models to explore their effect on the evolution of the ecological niche. Especially when the environment became temporally more predictive, (e.g. through temporal autocorrelation of the environmental conditions) this could highly affect the speed of local adaptation as well as the optimal niche width. If the interannual change would depend on the previous year, tolerance could e.g. be smaller, since no extreme interval between yearly environmental conditions could arise. Epigenetic effects could further shape an individuals niche, when parental environmental conditions were to be informative of expected offspring environmental conditions.

Adding sexual recombination to this could further enhance the possibilities of the model. It could either make adaptation to a changing habitat more difficult or ameliorate the adverse effects of change. Sexual recombination together with mate choice would e.g. speed up evolution when similar mates are chosen and speed up adaptation when mates with high expected fitness are chosen.

Overall, the model shed some light on crucial questions, but can also be easily expanded to include more variation in all of its attributes. This is one of the major advantages of IBMs. Enhancement of the study system is usually achievable and the different emerging patterns can help to understand which mechanisms are important to include to depict nature and which mechanisms lead to which patterns. This can help empiricists to select experimental setups and theoreticians to better predict the the possible consequences of global change and eventually the measures necessary to take to help slow it down.

10 Conclusion

In my thesis, I attempted to disentangle the effects of both spatial and temporal heterogeneity on the evolution of the environmental niche and dispersal. For this, I employed an individual based model (IBM), with escalating complexity. IBMs are an ideal tool to find possible evolutionary patterns, because they enable theoreticians to implement suspected and proven mechanisms and connections in evolutionary relevant time scales and with large datasets. I showed that both on a temporal as well as on a spatial scale, variation can be more influential then mean conditions. Indeed, the actual spatial configuration of this heterogeneity and the relationship between spatial and temporal heterogeneity affect the evolution of the niche and of dispersal probability more than landscape level mean conditions or interannual mean conditions. So far, there have been no modeling attempts, to include both the evolution of the environmental niche in two dimensions (optimum and niche width) and of dispersal probability in a spatio-temporally heterogeneous landscapes. However, the work is far from done and I presented various suggestions on what to do next. Including change in the temporal heterogeneity in spatially explicit models seems the next logical step, as well as including possible evolution of combinatorial and context-dependent dispersal strategies. These expansion could help the realism of the model and eventually shed light on its bearing on ecological global change predictions. For example species distribution models or extinction risk models would be more precise, if the included both spatial and temporal variation. The current modeling practices might not be sufficient to describe the possible outcomes of global change, because spatio-temporal heterogeneity and its influence on the formation of species' niches is too important to be ignored any longer.

IV | Bibliography

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V | Appendix

Affidativ

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I hereby confirm that my thesis entitled *Potential evolutionary responses to landscape heterogeneity and systematic environmental trends* is the result of my own work. I did not receive any help or support from commercial consultants. All sources and / or materials applied are listed and specified in the thesis.

Furthermore, I confirm that this thesis has not yet been submitted as part of another examination process neither in identical nor in similar form.

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Eidesstattliche Erklärung

Hiermit erkläre ich an Eides statt, die Dissertation *Mögliche evolutionäre Reaktionen auf Landschaftsheterogenität und systemische Umwelttrends* eigenständig, d.h. insbesondere selbständig und ohne Hilfe eines kommerziellen Promotionsberaters, angefertigt und keine anderen als die von mir angegebenen Quellen und Hilfsmittel verwendet zu haben.

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Ort, Datum **Unterschrift**

Publications

The following publications I authored as part of my doctoral thesis.

Sieger, Charlotte S., Cobben, Marleen M. P. and Hovestadt, Thomas (October 1, 2019). “Environmental change and variability influence niche evolution of isolated natural populations”. In: *Regional Environmental Change* 19.7, pp. 1999–802 2011. doi: 10.1007/s10113-019-01534-3.

Sieger, Charlotte S. and Hovestadt, Thomas (May 2020). "The degree of spatial variation relative to temporal variation influences evolution of dispersal" *accepted by Oikos.* doi: 10.1111/oik.07567.

Sieger, Charlotte S. and Hovestadt, Thomas (July 2020). "Landscape structure and spatio-temporal heterogeneity influence emigration rate more than emigration strategy" *in prep.*

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Declaration of author contributions

Statement of individual author contributions and of legal second publication rights

Sieger, C.S., Cobben, M.M.P. and Hovestadt, T. (October 1, 2019). "Environmental change and variability influence niche evolution of isolated natural populations". In: *Regional Environmental Change* 19.7, pp. 1999–802 2011. doi: 10.1007/s10113-019-01534-3.

Participated in	Author Initials, Responsibility decreasing from left to right		
Study Design	CSS	TH	MMPC
Methods Development	CSS	TH	MMPC
Data Collection	CSS		
Data Analysis and Interpretation	CSS	TH	
Manuscript Writing			
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Writing of Materials & Methods	CSS	TH	MMPC
Writing of Discussion	CSS	TH	MMPC
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Statement of individual author contributions to figures/tables/chapters included in the manuscripts

Chapter 5, Sieger, C.S., Cobben, M.M.P. and Hovestadt, T. (October 1, 2019). “Environmental change and variability influence niche evolution of isolated natural populations”. In: *Regional Environmental Change* 19.7, pp. 1999–802 2011. doi: 10.1007/s10113-019-01534-3.

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